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The *Canadian Journal of Fisheries and Aquatic Sciences* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, and *Journal of the Fisheries Research Board of Canada* 1938–79.

Editorial policy — The *Journal* publishes original research articles and notes, critical reviews, essays of opinion or hypothesis, letters, and book reviews in the broad field of fisheries science and management, marine and freshwater ecosystems, and aquatic biota relevant to Canada. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted and must not be published elsewhere except in abstract form or by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. The use of proprietary names does not imply endorsement of the product or company.

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Guide for authors — Guides for authors and typists appear in the first issue of each volume and are available free from the *Journal*.

Subscriptions — The *Journal* is issued monthly to form annual volumes of twelve numbers. Subscription rates are: Canada, $63.50 per year; other countries, $76.20. Single issues are $5.80 and $6.95, respectively. Supplements are $12 and $14.40, respectively. Orders must be sent directly to Supply and Services Canada, Hull, Que., Canada, K1A 0S9, and payment made in Canadian funds to "The Receiver General for Canada."

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Publié depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres: *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–79.

Politique de rédaction — Le *Journal* publie des articles et des notes fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse, des lettres et des comptes rendus de livres dans le vaste domaine des sciences halieutiques et de la gestion des pêches, des écosystèmes marins et d'eau douce, et des biocoenoses aquatiques pertinents au Canada. Toutes contributions en français ou en anglais sont acceptées sans restriction quant à la provenance, mais elles ne doivent pas avoir été produites ni avoir fait l'objet d'un copyright et ne doivent pas être publiées nulle part ailleurs sauf sous forme abrégée ou avec le consentement écrit du directeur. Le *Journal* décline toute responsabilité pour ce qui est des affirmations des collaborateurs. L'utilisation de noms de marque de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

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Canadian Journal of Fisheries and Aquatic Sciences

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ANNOUNCEMENTS/AVIS

Journal Receives Award for Excellence

In January 1983, I was honored to receive on behalf of the *Journal*, the first Special Group Award of Merit given by the American Institute of Fishery Research Biologists (AIFRB). This Award will be presented periodically to an organization, group, or team of fishery scientists who have made an outstanding contribution to fishery science or professionalism. Naturally, the present staff and former employees of CJFAS and its predecessors are delighted to be the first recipients. However, as I said in my remarks of acceptance, and in the short history of the *Journal* prepared for AIFRB's Newsletter, *BRIEFS*, the success of any research publication depends on the quality of articles submitted by authors and the caliber of advice provided by reviewers, in addition to the dedication of its staff.

On the recommendation of the Editorial Board, the remarks of the President of AIFRB, Bernard E. Skud, the Award, and my remarks of acceptance are reproduced in this issue, along with a reprint of the short History of the *Journal* prepared earlier.

J. WATSON
Editor-in-Chief

AIFRB Group Award

Presentation by Bernard E. Skud, President of the American Institute of Fishery Research Biologists (AIFRB), South Ferry Road, Narragansett, RI 02882.

I'm pleased to be here in Winnipeg and to participate in the Canadian Conference For Fisheries Research (CCFFR). Both the location and the conference are particularly appropos for the purpose of my attendance, which is to present an award

Certificat d'excellence au *Journal*

J'avais l'honneur, en janvier 1983, de recevoir au nom du *Journal* le premier certificat d'excellence spécial décerné à des groupes par l'*American Institute of Fishery Research Biologists* (AIFRB). Cette marque de distinction sera présentée périodiquement à un organisme, groupe ou équipe de scientifiques des pêches qui auront contribué de façon exceptionnelle à la science ou au professionnalisme halieutiques. Point n'est besoin de souligner que les équipes présente et passées du *Journal canadien des sciences halieutiques et aquatiques* et de ses prédécesseurs sont heureuses d'en être les premiers récipiendaires. Cependant, comme je le mentionnais dans mes remarques d'acceptation et dans le bref historique du *Journal* paru dans le Bulletin de l'AIFRB, *BRIEFS*, le succès de toute publication scientifique dépend de la qualité des articles qui lui sont soumis et du calibre des conseils que lui offrent les censeurs, sans compter le dévouement de son personnel.

Conformément à la recommandation du Conseil de rédaction, nous reproduisons dans la présente livraison les remarques du président de l'AIFRB, Bernard E. Skud, le certificat lui-même, mes remarques d'acceptation et enfin la version française du bref historique du *Journal* publié antérieurement.

J. WATSON
Rédacteur en chef

Certificat d'excellence de l'AIFRB

Présentation de Bernard E. Skud, président de l'*American Institute of Fishery Research Biologists* (AIFRB), South Ferry Road, Narragansett, RI 02882.

Je suis heureux d'être à Winnipeg et de participer à la

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from AIFRB to the *Canadian Journal of Fisheries and Aquatic Sciences*. I want to say a few words about the Award, about the *Journal*, and about fishery journals in general.

The objectives of this Conference mesh well with the objectives of AIFRB which was incorporated in 1956 to advance the theory and practice of Fishery Biology and related sciences; to promote conservation and proper utilization of fishery resources, and to establish and maintain high professional standards by the recognition of achievement and competence. The Institute also encourages professional involvement in public affairs and adherence to a code of professional ethics.

AIFRB annually solicits nominations of papers published by students and makes a $750 award to the student whose paper is selected as the best. AIFRB periodically awards certificates of achievement to individuals who have contributed in an exceptional way to the profession. This past year the Board of Directors decided to institute a new award which would recognize achievement by a group. The Board served as the selection committee for the first recipient and the unanimous choice was the *Canadian Journal of Fisheries and Aquatic Sciences*. The tenor of the Board's selection is explicitly expressed in the wording of the Award:

Conférence canadienne relative à la recherche sur les pêches en eau douce (CCRP). L'endroit lui-même et la Conférence sont tous deux pertinents au but de ma visite qui est de présenter, de la part de l'AIFRB, un certificat d'excellence au *Journal canadien des sciences halieutiques et aquatiques*. Je voudrais dire quelques mots au sujet de cette marque de distinction, du *Journal* et enfin des périodiques halieutiques en général.

Les objectifs de la présente Conférence s'accordent bien avec ceux de l'AIFRB, incorporée en 1956 dans le but de promouvoir la biologie des pêches et sciences connexes, tant dans leur aspect théorique que pratique; de promouvoir la conservation et la bonne utilisation des ressources halieutiques; et d'établir et maintenir un haut niveau de professionnalisme en récompensant le succès et la compétence. L'Institut encourage également la participation professionnelle de ses membres aux affaires publiques et l'adhésion à un code de la morale professionnelle.

Chaque année, l'AIFRB sollicite la mise en candidature d'articles publiés par des étudiants et accorde une récompense de 750 $ à l'étudiant dont l'article a été jugé le meilleur. L'AIFRB décerne périodiquement des certificats de mérite aux individus dont la contribution à la profession a été exceptionnelle. L'année dernière, le Conseil des directeurs décidait d'établir une nouvelle distinction pour souligner une réussite d'un groupe. Le Conseil a agi comme comité de sélection du premier récipiendaire, et le choix unanime a été le *Journal canadien des sciences halieutiques et aquatiques*. Les mots qui accompagnent le certificat reflètent bien les sentiments qui ont présidé au choix du Conseil :

THE AMERICAN INSTITUTE
OF
FISHERY RESEARCH BIOLOGISTS

SPECIAL GROUP AWARD OF MERIT

IN RECOGNITION OF THE OUTSTANDING CONTRIBUTION TO FISHERY SCIENCE, THE STAFF OF

THE CANADIAN JOURNAL OF FISHERIES AND AQUATIC SCIENCES

FORMERLY

THE JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

IS HEREBY COMMENDED BY THE AMERICAN INSTITUTE OF FISHERY RESEARCH BIOLOGISTS. FOR NEARLY 50 YEARS, THIS EXTRAORDINARY TEAM EFFORT HAS ESTABLISHED AND MAINTAINED A STANDARD OF SCIENTIFIC EXCELLENCE THAT HAS GAINED INTERNATIONAL ACCLAIM. ALL OF THE EDITORS, STAFF AND THE ADMINISTRATORS OF THE CANADIAN GOVERNMENT WHO SUPPORTED THIS INITIATIVE SHARE IN THIS SUCCESS AND CAN BE JUSTLY PROUD OF THEIR ACCOMPLISHMENTS. THE INSTITUTE ALSO RECOGNIZES THE ROLE OF THE JOURNAL IN FURTHERING THE STANDARDS OF PROFESSIONALISM AMONG FISHERY SCIENTISTS.

Bernard E. Skud
PRESIDENT

SEAL

G. Hubert Powles
SECRETARY

This recognition of excellence is echoed by the *Journal*'s wide circulation and by its world-wide distribution of contributors. In one sense, AIFRB's Award to the *Journal* is formalizing what most fishery biologists already recognize and acknowledge.

Other attributes of the *Journal* should also be mentioned — one which I consider particularly important is its record of flexibility to adapt to changes of emphasis in the field of fishery biology as evidenced by its timely scientific articles and by the provocative *Perspectives*. The long tenure of the *Journal*'s success is all the more remarkable when one considers the economic and political changes which the *Journal* has weathered. Other scientific outlets have not done as well and there is a lesson to be learned from their experience. Fishery scientists and their professional societies cannot be complacent about the success of the *Journal* and must always be ready to support it vigorously and defend its status, for scientific outlets of this caliber are essential to the further development and recognition of our profession.

With that, it is an honor for me on behalf of AIFRB to present its first Group Award of Merit to the Editor-in-Chief of the *Canadian Journal of Fisheries and Aquatic Sciences* (and Director of the Scientific Information and Publications Branch), Jeffrey Watson.

AIFRB Award — Acceptance Remarks

Those of us who help put the *Journal* together are delighted that CJFAS is the first to be selected for this recognition by such an eminent group as the American Institute of Fishery Research Biologists. The history of the *Journal* is a long one, spanning over 80 years. This history is documented in the October 1982 issue of the AIFRB Newsletter, *BRIEFS*.

It is a personal honor to be the one to receive the award. The status of the *Journal*, however, depends not on one person but on many factors: the dedication and vision of those presently and formerly associated with the *Journal*; the quality of articles submitted by authors; and the quality of advice provided by reviewers, to mention a few.

The fact that the *Journal* is the most highly cited publication of its kind in the world, that a good number of papers have become Citation Classics, and that its paid circulation is large, is evidence that we have been fortunate in receiving top quality manuscripts and advice from you, the scientific community. You constitute the *Journal*'s lifeblood; we are the health care practitioners who keep the organism healthy.

So to the scientific community, of which those of you present are but a sample, I say: Our success is your success and we are delighted to share it with you. We will continue to aspire to excellence, and with your help we will achieve it.

J. WATSON

History of the *Journal*[1]

The roots of the *Canadian Journal of Fisheries and Aquatic Sciences* reach back to the beginning of this century and the

[1]Reprinted from AIFRB, *BRIEFS*, Vol. 11, No. 5, October 1982.

Le grand tirage du *Journal* et la contribution d'auteurs répartis dans le monde entier témoignent de l'excellence de ce périodique. En lui accordant cette distinction, l'AIFRB ne fait en quelque sorte que formaliser ce que la plupart des biologistes en pêcheries reconnaissent déjà.

Je devrais également mentionner d'autres qualités du *Journal* — une entre autres que je considère comme particulièrement importante est la flexibilité qu'il a démontrée pour s'adapter aux divers courants de la biologie des pêches, comme le démontrent bien ses articles scientifiques à propos et ses *Perspectives* provocatrices. La pérennité du succès de ce périodique est d'autant plus remarquable qu'il a dû survivre à bien des changements économiques et politiques. Ce ne fut pas toujours le sort d'autres publications scientifiques, et l'expérience de ces dernières devrait être une leçon pour nous tous. Il ne faudrait toutefois pas que les scientifiques halieutiques et leurs sociétés professionnelles se parent d'un optimisme béat devant le succès du *Journal*; il leur faudra toujours être en mesure de l'appuyer et le défendre vigoureusement, car des publications scientifiques de ce calibre sont essentielles au développement et à la réputation de notre profession.

Ceci dit, c'est pour moi un honneur de présenter, au nom de l'AIFRB, son premier certificat d'excellence pour groupes au rédacteur en chef du *Journal canadien des sciences halieutiques et aquatiques* (et directeur de la Direction de l'information et des publications scientifiques), Jeffrey Watson.

Certificat d'excellence de l'AIFRB Remarques d'acceptation

Ceux parmi nous qui travaillent à la rédaction du *Journal* se réjouissent que le JCSHA soit le premier récipiendaire d'une marque de distinction décernée par un organisme aussi éminent que l'*American Institute of Fishery Research Biologists*. Le *Journal* a une longue histoire couvrant plus de 80 ans. J'en présente un résumé dans la livraison d'octobre 1982 du Bulletin de l'AIFRB, *BRIEFS*.

C'est pour moi un honneur personnel d'accepter cette distinction. Le calibre du *Journal*, cependant, ne dépend pas d'une personne en particulier, mais plutôt de plusieurs facteurs : dévouement et imagination des personnes présentement et jadis associées au périodique; qualité des articles qui lui sont soumis; et bons conseils des censeurs, pour ne mentionner que quelques-uns.

Le fait que le *Journal* soit le périodique de son genre le plus fréquemment cité dans le monde, qu'un bon nombre des articles qui y sont publiés deviennent des « classiques de citation » et que son tirage payé soit aussi grand témoigne de la qualité supérieure des manuscrits et des conseils que nous avons la bonne fortune de recevoir de vous tous, la communauté scientifique. Vous êtes le principe de vie du *Journal*; nous en sommes les praticiens qui voyons à ce que l'organisme se maintienne en bonne santé.

À toute la communauté scientifique, dont seulement un échantillon est ici présent, je dis : Notre succès est le vôtre, et nous sommes heureux de le partager avec vous. Nous continuerons de viser haut et, avec votre aide, nous réussirons.

J. WATSON

start of organized fisheries research in Canada. In 1899 the Board of Management of the Marine Biological Station, directed by Dr. E. E. Prince began investigations at St. Andrews, N.B. from a moveable laboratory that was designed to be towed from one location to another along the shoreline. Less than two years later the first of the *Journal*'s predecessors appeared as a supplement to the 32nd Annual Report of the Department of Marine and Fisheries. Seven articles constituted the first "*Contributions to Canadian Biology*" and described research on both fundamental and applied problems.

From these small beginnings, an occasional publication intended primarily to record the investigations of the Board of Management and a few visiting academics has grown into one of the leading international periodicals for communicating research results in fisheries and aquatic sciences.

In 80 years the *Journal*'s title has changed five times:

- Contributions to Canadian Biology 1901-1925
- Contributions to Canadian Biology and Fisheries 1926-1934
- Journal of the Biological Board of Canada 1934-1937
- Journal of the Fisheries Research Board of Canada 1938-1979
- Canadian Journal of Fisheries and Aquatic Sciences 1980-

From the very beginning articles spanned most disciplines in marine and freshwater research. Editorial boards and advisors were drawn from universities and government across Canada — a profitable linkage between Government and Academia that continues today. By 1934 the publication had clearly become a periodical directed mainly to other scientists, so the name was changed to reflect its status as a repository of original research. In 1937 when the Board's name changed so did that of the *Journal*. When the Fisheries Research Board of Canada was dissolved in the mid '70's the inevitability of another name change was apparent. The current name is free of organizational connotations and reflects the broad scope that has always been characteristic of the *Journal* so further name changes are not anticipated. Although the scope has been similar over the years, the content of the *Journal* has changed as fisheries and aquatic sciences evolved from descriptive approaches to more sophisticated experimental and holistic investigations of aquatic systems.

The Board attached considerable importance to publications; Prince, the first Chairman, was also the first editor and subsequently other Chairmen and Senior Members of the Board became editors. The appointment of Dr. W. E. Ricker as editor in 1950 had a profound influence on the development of the *Journal of the Fisheries Research Board of Canada*. Ricker set about getting the best Board work published, encouraging publication of important work from elsewhere, particularly the United States, and making sure that the *Journal* was distributed widely. Ricker set up an extensive publication exchange program for both the *Journal* and the Bulletin Series. Institutions in Developing Countries with no publications to exchange received the *Journal* as a gift. This program was continued actively by Dr. J. C. Stevenson, the first full time editor, and ensured that much of Canadian fisheries science reached all corners of the globe. The distribution of the *Journal* to so many marine and freshwater laboratories played a significant role in enhancing Canada's reputation in fisheries science.

Since its inception, the growth and influence of the *Journal*

Historique du *Journal*[1]

Le *Journal canadien des sciences halieutiques et aquatiques* naquit au début du siècle, en même temps que la recherche halieutique organisée au Canada. En 1899, le Conseil de gestion de la Station de biologie marine, sous la direction du D[r] E. E. Prince, commençait des recherches à St. Andrews (N.-B.) dans un laboratoire flottant, conçu pour être remorqué d'un endroit à l'autre le long de la côte. Moins de deux ans plus tard, apparut le premier des prédécesseurs du *Journal*, sous la forme d'un supplément au 32[e] Rapport annuel du ministère de la Marine et des Pêcheries. Y étaient publiés sept articles qui constituèrent les premières « *Contributions to Canadian Biology* ». On décrivait dans ces articles des recherches sur des problèmes tant fondamentaux qu'appliqués.

De ces modestes débuts, une publication sporadique dont le premier objectif était de consigner les recherches du Conseil de gestion et de quelques universitaires en visite se développa et devint un des principaux périodiques internationaux en sciences halieutiques et aquatiques.

Au cours des 80 ans de son existence, le *Journal* a connu cinq titres différents :

- Contributions to Canadian Biology 1901-1925
- Contributions to Canadian Biology and Fisheries 1926-1934
- Journal of the Biological Board of Canada 1934-1937
- Journal of the Fisheries Research Board of Canada 1938-1979 (Journal de l'Office des recherches sur les pêcheries du Canada)
- Canadian Journal of Fisheries and Aquatic Sciences 1980- (Journal canadien des sciences halieutiques et aquatiques)

Dès le début, on y publiait des articles couvrant la plupart des disciplines de recherches en mer et en eau douce. Des conseils de rédaction et des aviseurs furent recrutés à même le personnel des universités et des gouvernements par tout le Canada — une union gouvernements–universités très fructueuse qui dure toujours. Dès 1934, la publication était clairement devenue un périodique qui s'adressait surtout aux autres scientifiques. Le nom en a donc été changé pour refléter sa vocation comme dépôt de recherches originales. En 1937, une appellation nouvelle pour l'Office entraîna un changement pour le *Journal* également. Avec la dissolution de l'Office des recherches sur les pêcheries du Canada au milieu des années 1970, un autre changement de nom était devenu inévitable. Le titre actuel ne réfère à aucun organisme et reflète le vaste champ d'action qui a toujours été la caractéristique du *Journal*. On ne prévoit donc pas d'autres changements. Bien que la portée du *Journal* soit demeurée la même au cours des ans, son contenu a varié à mesure les sciences halieutiques et aquatiques, de descriptives qu'elles étaient dans leur approche, évoluaient en des recherches expérimentales et holistiques plus sophistiquées sur les systèmes aquatiques.

L'Office a toujours accordé beaucoup d'importance à la publication des résultats; son premier président, Prince, était aussi son premier rédacteur. Par la suite, d'autres présidents et principaux membres de l'Office remplirent ce rôle. La nomination du D[r] W. E. Ricker comme rédacteur en 1950 eut une profonde influence sur le développement du *Journal de*

[1]Reimprimé de l'AIFRB, *BRIEFS*, vol. 11, n° 5, octobre 1982.

increased greatly. To illustrate, an average of 13 articles per year appeared up to 1950, 51 articles per year between 1950-1962, and 224 articles per year since 1962. But numbers tell an incomplete story. Despite firm editorial policies, increased rejection rates and introduction of page charges, paid subscriptions as well as manuscript submissions have increased dramatically. A change from bimonthly to monthly publication in 1966 and continued maintenance of high standards gave another boost to the *Journal*, doubling its exposure to the readership. During the '60's and '70's *Journal* papers won a number of awards from the Wildlife Society of America. Several papers have been identified as Citation Classics in *Current Contents*, and the *Science Citation Index* shows that the *Journal*'s citation rates and impact is increasing every year.

In the '70's a deliberate effort was made to build upon Ricker's example and broaden the intellectual scope of the *Journal* by introducing "*Perspectives*" which are broadly based essays of opinion or hypotheses and by publishing sound critical reviews. At the same time the *Journal* published Special Issues on specific topics of high scientific interest or the proceedings of major symposia on critical areas of concern. Many of these special issues have become classics and are the benchmark publications on which future research or management strategy can be based.

On behalf of present and past employees of the *Journal*, I thank the American Institute of Fishery Research Biologists for selecting the *Journal* as the first recipient of its Special Group Award of Excellence. Much of the success of any journal is due to the authors it attracts, the quality of advice provided by reviewers to help editors evaluate contributions and the dedication of its staff. *The Canadian Journal of Fisheries and Aquatic Sciences* and its predecessors have been fortunate in receiving top quality manuscripts and advice from the scientific community and have been blessed by a staff dedicated to excellence.

J. WATSON

l'Office des recherches sur les pêcheries du Canada. Ricker a vu à ce que soient publiées les meilleures recherches de l'Office, tout en encourageant la publication de travaux menés ailleurs, surtout aux États-Unis, et enfin s'assurant que le *Journal* était largement distribué. Il mit sur pied un important programme d'échanges des publications, tant pour le *Journal* que pour la série des *Bulletins*. Les pays en voie de développement qui n'avaient pas de publications à échanger reçurent le *Journal* à titre gratuit. Le Dr J. C. Stevenson, le premier rédacteur à plein temps, poursuivit activement ce programme et s'assura que les résultats des recherches halieutiques canadiennes soient répandus dans tous les coins du globe. La distribution du *Journal* parmi autant de laboratoires maritimes et d'eau douce contribua pour beaucoup à rehausser la réputation du Canada en sciences halieutiques.

La croissance et le rayonnement du *Journal* ont, au cours des ans, pris beaucoup d'ampleur. Comme exemple, jusqu'en 1950, une moyenne annuelle de 13 articles étaient publiés, 51 entre 1950 et 1962, et 224 depuis 1962. Ces chiffres ne représentent toutefois pas le tableau complet. En dépit de politiques éditoriales fermes, d'un taux de refus plus élevé et de l'introduction de frais par page publiée, les abonnements payés ainsi que le nombre de manuscrits soumis ont augmenté de façon dramatique. Le changement d'une publication paraissant tous les deux mois en une publication mensuelle en 1966 ainsi que la qualité toujours supérieure des articles contribuèrent à accroître la popularité d'un périodique atteignant le lecteur à fréquence double. Dans les années 60 et 70, les articles publiés dans le *Journal* se méritèrent plusieurs marques de distinction de la *Wildlife Society of America*. Plusieurs ont été reconnus comme classiques de citation dans « *Current Contents* ». On voit dans le *Science Citation Index* que le taux et l'impact des citations du *Journal* augmentent d'année en année.

Un effort délibéré a été fait dans les années 70 pour amplifier l'oeuvre de Ricker et élargir la portée intellectuelle du *Journal*, en premier lieu par l'introduction des « *Perspectives* », essais généraux portant sur une opinion ou des hypothèses et, en second lieu, par la publication de comptes rendus bien étayés d'ouvrages nouvellement parus. Le *Journal*, vers le même temps, consacrait des numéros spéciaux à des sujets d'intérêt scientifique particulier ou aux actes de colloques importants consacrés à des questions critiques. Plusieurs de ces numéros spéciaux sont devenus des classiques et servent de points de repère à partir desquels orienter la recherche future ou encore les stratégies de gestion.

Au nom des employés présents et passés du *Journal*, je remercie l'*American Institute of Fishery Research Biologists* pour avoir choisi le *Journal* comme premier récipiendaire de son certificat d'excellence spécial pour groupes. Le succès de tout périodique dépend en grande partie des auteurs qu'il attire, de la qualité des conseils que lui offrent les censeurs et qui aident les éditeurs à évaluer les manuscrits et, enfin, du dévouement de son personnel. Le *Journal canadien des sciences halieutiques et aquatiques* a eu la bonne fortune de recevoir manuscrits et conseils de qualité supérieure de la part de la communauté scientifique et d'être desservi par un personnel qui a toujours visé à l'excellence.

J. WATSON

Adaptive Flexibility in the Foraging Behavior of Fishes[1]

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Flexibility is an important adaptive feature of the foraging behavior of fishes, because most natural environments vary both spatially and temporally. Fish should respond to low levels of food availability by altering their behavior in ways which ensure higher feeding rates, larger feeding territories, and broader diets. It is shown that the gastric sensation of hunger and its rate of change may act as appropriate cues to food availability, and observed hunger-motivated changes in feeding behavior can produce all of these predicted effects. Data are presented to show that juvenile coho salmon (*Oncorhynchus kisutch*) alter their behavior in an adaptive manner when faced with variable degrees of threat of competition from territorial intruders, and of risk of predation. A review of similar studies on other species supports the generality of these results. Learning is an important mechanism providing behavioral flexibility, and changes in fish feeding behavior with experience are summarized. A graphical model is developed to show that these changes can result in training biases and food specialization. Learning also results in increased feeding rates. The consequences of these observations for the development of refined models of foraging are discussed.

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Chez les poissons, la flexibilité du comportement alimentaire est un trait adaptatif important car la plupart des environnements naturels varient de façon spatiale et temporelle. Les poissons devraient réagir à de bas niveaux de nourriture disponible en altérant leur comportement de façon à s'assurer un taux plus élevé d'alimentation, des territoires d'alimentation plus grands et une diète plus diverse. Il est démontré que la sensation gastrique de la faim et son taux de changement peuvent agir comme indices de la disponibilité de nourriture, et que les changements du comportement alimentaire motivé par la faim que l'on a observé peuvent produire ces effets comme prévu. Des données démontrent que de jeunes saumons argentés (*Oncorhynchus kisutch*) modifient leur comportement de façon adaptative lorsqu'ils font face à des degrés variables de menace de compétition dus à des intrus de leur territoires, et des risques de predation. Une revue d'études similaires sur d'autres espèces supporte la généralité de ces résultats. Un mécanisme important qui produit une flexibilité comportementale est l'apprentissage, et des changements dans le comportement alimentaire reliés à l'expérience des poissons sont résumés. Un modèle graphique est développé pour montrer que ces changements peuvent aboutir à des biais d'entraînement et à une spécialisation alimentaire. L'apprentissage résulte également en une augmentation du taux d'alimentation. Les conséquences de ces observations pour le développement de modèles raffinés du comportement alimentaire sont discutés.

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FISH, like other animals, must make numerous decisions while foraging. At a macro-level, they must decide where to feed and what types of prey to feed upon. At a micro-level, decisions are required concerning such things as how fast to approach a particular prey item, or how aggressive to be towards a particular territorial intruder. That individual which makes the more correct decisions will feed more efficiently and have higher fitness (expected lifetime reproductive output) relative to other members of the population.

A major problem faced by a foraging fish is that its environment is characterized by heterogeneity in both space and time, and a decision appropriate in one set of circumstances may be inappropriate in others. Some of this variability will be patterned (e.g. diel changes in food availability) and therefore predictable to the fish, but other types of variation will be stochastic and unpredictable. Relevant examples of this latter type of variation include local food availability, the type of territorial intruder encountered, and risk of predation in a particular locality.

Given this variability, it is reasonable to expect that for-

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aging fishes will have developed mechanisms which allow them to attune their foraging behavior to extant environmental circumstances. This implies two things: first, the ability to collect relevant information and thus be sensitive to variation in key environmental parameters; and second, foraging behaviors sufficiently plastic to respond to such information. Recently, a considerable number of studies have investigated these aspects of fish foraging behavior. The primary purpose of this paper is to review such studies, especially those carried out in my laboratory on juvenile coho salmon (*Oncorhynchus kisutch*), and show that fish foraging behavior is characterized by adaptive flexibility.

Much of my own research has concerned "distance-contingent" behavior, behavior shown only when a particular distance separates the fish and a relevant stimulus object (e.g. food item, competitor, predator). Such behavior implies response thresholds, and because thresholds may be altered both by the internal motivational state of the animal and by features of the external environment, they are potentially very important in allowing flexibility.

The last 15 yr have seen the extensive application of optimization techniques to the study of foraging behavior. These hypothesize an optimality criterion (some quantity the forager is attempting to maximize) and then predict an optimal set of behaviors, or optimal foraging strategy. The approach has been extremely successful as a means of organizing knowledge of foraging behavior, and of directing research. However, applications of the technique to date can be criticized on several grounds (Krebs et al. 1981). Firstly, most optimality techniques presently used by ecologists deal with static rather than dynamic situations; they do not include changes in the animal's motivational state (and consequent behavior) resulting from feeding. Secondly, they assume perfect knowledge on the part of the forager; for example, the animal is assumed to know the availability of various food types and their relative profitabilities, and little attention has been paid to how an animal acquires such information. Thirdly, the optimality criterion (usually assumed to be net rate of energy intake) is probably overly simplistic in many circumstances; many foragers will need to trade this off against other demands, e.g. the need to avoid predators. Partly for these reasons, successful tests of optimality predictions have been almost entirely laboratory based. Field tests have been much less successful (Schluter 1981), probably because real environments vary both spatially and temporally as discussed above.

I will largely avoid the optimality approach in this paper. Rather than predicting fish foraging behavior from some assumed criterion, I will emphasize empirical evidence of what fish actually achieve. It is frequently difficult to argue convincingly that a particular behavior is optimal in any event, as this depends on the function which the investigator assumes the animal is attempting to maximize. However, it is usually possible to argue less rigorously that the observed flexibility is adaptive, in that it will contribute to increased fitness. In the sections that follow, I will apply this approach to examining how fish respond to different levels of three critical ecological variables: food availability, threat of competition, and risk of predation. In the final section I will discuss how fish alter their behavior as a result of experience, as this is an obvious means of adjusting behavior to particular environmental conditions.

Food Availability

Spatial and temporal variations in food availability are clearly of particular relevance from the viewpoint of a foraging fish. It is of paramount importance for the forager to monitor food availability, and to respond adaptively to variation; I will examine these points in turn.

Monitoring Food Availability

It is unlikely that a fish can visually assess the numbers and energetic contents of prey available, or count and weigh prey as eaten, and integrate this information over time to estimate food availability. However, the fish can use stretch receptors to monitor gut fullness, and this gastric sensation of hunger may be a reliable cue to food availability in many instances.

Hunger motivation in fishes undoubtedly has two components — gastric (stomach fullness) and metabolic (levels of circulating metabolites). Accordingly, hunger can be manipulated in two ways — via satiation (short-term) or deprivation (long-term). That stomach fullness is not a complete descriptor of hunger is indicated by experiments such as those by Beukema (1968): variation in length of a preceding deprivation period influenced the amount eaten by threespine sticklebacks in the 1st hour of feeding, even though all of the fishes' stomachs were equally empty at the start of the trial. However, because fish are unlikely to be entirely deprived of food for long periods of time in nature, the amount of food in the gut is probably the best operational measure of hunger and probably corresponds best to the sensation experienced by a fish. During a feeding session, as the gut fills, satiation increases and perceived hunger declines. The question is whether food availability and hunger defined in this way are correlated, and whether hunger (or its first derivative) can therefore be used by a fish as an estimate of food availability. Charnov (1976) argued that this would be possible once an animal reaches equilibrium with its food supply, i.e. once intake rate equals loss rate and the amount of food in the gut remains constant. This equilibrium requirement may be unnecessarily restrictive, however.

Although feeding is a discontinuous process, Elliot and Persson (1978) have shown that the amount of food in a fish's stomach at any point in time (S_t) after starting with an empty gut (i.e. $S_o = 0$) can be predicted from the continuous approximation:

$$(1)\quad S_t = \frac{F}{R}(1 - e^{-Rt})$$

where F is the feeding rate (assumed to be constant) and R the evacuation (digestion) rate. The rate of change of hunger is then:

$$(2)\quad \frac{dS_t}{dt} = Fe^{-Rt}.$$

From rearrangement of equation (1)

$$(3)\quad Fe^{-Rt} = F - RS_t$$

and therefore, substituting (3) into (2):

$$(4)\quad \frac{dS_t}{dt} = F - RS_t.$$

If a steady state is reached dS_t/dt becomes 0 and S_{eq} (the amount of food in the gut at equilibrium) equals F/R. Thus, under the assumption that F is constant over time and directly related to food availability, the amount of food in the gut at equilibrium and equilibrium hunger (gut capacity less S_{eq}) are also directly related to food availability. This agrees with Charnov's (1976) conclusion.

Even if a steady state is not reached, at any given time the rate of filling of the gut is also directly related to F and therefore to food availability (eq. 2). Also of interest is the fact that the rate of filling of the gut is a good indicator of the ultimate steady state level, for substituting $R \cdot S_{eq} = F$ into eq. (4) and rearranging gives:

$$(5)\quad \frac{dS_t}{dt} + RS_t = RS_{eq}.$$

This means that at any time after beginning feeding, a fish can predict its ultimate steady state gut fullness from present fullness and rate of filling. The total amount of food consumed in a period t (C_t), assuming a constant feeding rate, is simply (Elliott and Persson 1978):

$$(6)\quad C_t = Ft.$$

Because F ($=R \cdot S_{eq}$) can be estimated from gut volume and its first derivative (eq. 5), a fish can in theory predict the total value of a patch which it has entered and use this information in deciding whether to leave or stay. This is a potentially powerful sampling rule, providing that food availability is relatively constant during the sampling period. Among other things this implies that a patch is not depleted by the fish; if that occurs, perceived hunger will lag too far behind current conditions to be of much use (Ebersole and Wilson 1980).

Unfortunately, for reasons to be discussed below, even when food availability is constant over time, a fish's feeding rate may not be; it may often be some decreasing function of satiation (S_t). Three possibilities are:

$$(7)\quad F = F_{max} - aS_t \text{ (linear)}$$

$$(8)\quad F = F_{max} - aS_t^b \text{ (power)}$$

and

$$(9)\quad F = F_{max} - ae^{S_t b} \text{ (exponential)}$$

where F_{max} is the feeding rate of a maximally hungry fish (i.e. at $S_t = 0$). Substituted into equation (1) the power and exponential forms produce equations which are analytically insolvable for S_t, and therefore cannot be differentiated. However S_t and F_{max} are correlated, suggesting that hunger can still be used by a fish as a measure of food availability, albeit a complex one requiring more information (knowledge of the constants a and b, and time).

The linear case is solvable, producing the rather complex equations:

$$(10)\quad S_t = \frac{F_{max}(1 - e^{-Rt})}{R + a(1 - e^{-Rt})}$$

and

$$(11)\quad \frac{dS_t}{dt} = \frac{R \cdot F_{max}}{R + a(1 - e^{-Rt})} e^{-Rt}\left[1 - \frac{a(1 - e^{-Rt})}{R + a(1 - e^{-Rt})}\right].$$

Hunger and rate of change of hunger at any point in time are again directly correlated with food availability, assuming that F_{max} is directly related to it. Thus, even when feeding rate changes with time, the fish can monitor food availability using the sensation of gastric hunger.

Hunger and Feeding Behavior

The effect of hunger on feeding behavior is usually investigated by examining changes in behavior as a fish satiates during a single feeding trial, and several such effects are listed in Table 1. A word of caution is in order, however, as other aspects of motivation may change during a feeding sequence. For example, Thomas (1977) found that the probability of a

Table 1. Effects of satiation on fish foraging behavior.

Behavior affected	Species	Source
1. *Searching decreases*		
Response to prey odor	Yellowfin tuna (*Thunnus albacares*)	Atema et al. (1980)
Swimming speed	Threespine stickleback (*Gasterosteus aculeatus*)	Beukema (1963)
Reactive distance	Lake trout (*Salvelinus namaycush*)	Confer et al. (1978)
2. *Conditional probabilities decrease*		
Grasp/discovery	Threespine stickleback	Beukema (1968)
Eat/grasp	Threespine stickleback	Beukema (1968)
Eat/encounter	Pumpkinseed sunfish (*Lepomis gibbosus*)	Colgan (1973)
Attack/approach	Bluegill sunfish (*Lepomis macrochirus*)	Chiszar and Windell (1973)
Attack/response	Skipjack tuna (*Katsuwonus pelamis*)	Magnuson (1969)
Eat/attack	Threespine stickleback	Tugendhat (1960)
3. *Handling time increases*	Bluegill sunfish	Werner (1974)
	Threespine stickleback	Beukema (1968)
	Fifteenspine stickleback (*Spinachia spinachia*)	Kislalioglu and Gibson (1976)

stickleback eating an encountered prey declines rapidly when plotted against the cumulative number of rejected prey, but not when plotted against the number eaten. The data in Table 1 are the best available at this time, however. The effects of hunger will be opposite those of satiation. Therefore, as hunger increases, both search rate and the conditional probabilities for various stages in the predation process (e.g. $p_{eat/attack}$ is the probability of eating an attacked prey) will increase. The average handling time per prey capture will decrease, both directly and because fewer encounters will be unsuccessful in terms of ultimate ingestion.

These hunger-motivated changes will have several consequences which will be adaptive for fish faced with low levels of food availability. Firstly, the encounter rate with prey while searching will increase. Secondly, more time will be available for searching as average handling time declines. This will result in higher attack rates, as documented by Ware (1972) and Heller and Milinski (1979) in hungry rainbow trout and sticklebacks, respectively. A further consequence of hunger will be an increased profitability (net energy value per unit of handling time) for each prey captured. This results from both decreased handling time and increased net energy value (assuming that handling cost is proportional to handling time).

A number of field observational studies (e.g. Doble and Eggers 1978) and the experimental studies of Ivlev (1961), Beukema (1963), Werner and Hall (1974), and Kislalioglu and Gibson (1975) suggest that many fish broaden their diet to include less preferred prey as the availability of the preferred prey declines (and hunger consequently increases). Diet broadening will be an adaptive response if it increases the fish's net rate of energy return. This could occur, for example, if the hunger-induced behavioral changes were more marked for prey not already included in the diet of well fed fish, i.e. if the change in profitability were greater for less preferred prey. This would be likely if the profitability of the preferred prey were already near its maximum level. I am aware of no data bearing on this question, although those of Olla et al. (1970) are suggestive. These authors showed that the capture success of feeding bluefish (*Pomatomus saltatrix*) declines during a feeding session, but returns to a high level if the original small prey are replaced by larger ones. This suggests a hunger-motivated change in behavior which is prey type dependent. Broadening of the diet would also increase the rate of energy intake, and thus be adaptive, if the change in encounter rate with the preferred prey were small relative to changes in profitability, even if these were proportional for all prey types. It is therefore of interest that several authors have been unable to document changes in reactive distance (an important determinant of encounter rate) with hunger: Ware (1971a) for rainbow trout; Dunbrack and Dill (1983) for juvenile coho salmon; and Beukema (1968) for threespine sticklebacks over most hunger levels. The data of Confer et al. (1978) are based on a single lake trout — a second individual showed no such effect.

Optimal foraging models allow predictions to be made concerning which sorts of behavioral changes should lead to diet broadening, i.e. when this response will increase net energetic intake rate. However, most current optimality models ignore the metabolic cost of searching and therefore are not useful when searching rate (and consequently cost) increases with hunger (R. L. Dunbrack unpublished data).

Aggressive behavior and territorial defense can also be considered part of a fish's foraging strategy, to the extent that food is the resource contested or defended. For example, the optimal territory size will be that which maximizes energy intake rate, and energetic models predict that an increase in food availability should decrease this optimal size (Dill 1978a). Although various experimental protocols and feeding regimes have produced conflicting data on the response of salmonid aggression and territory size to manipulations of the food supply (reviewed in Dill et al. 1981), we have demonstrated that the territories of juvenile coho are smaller in habitats rich in benthic foods (Dill et al. 1981). Similar results have been reported for rainbow trout *Salmo gairdneri* (Slaney and Northcote 1974), surf-perch *Embiotoca jacksoni* (Hixon 1981), and male damselfish *Eupomacentrus leucostictus* (Ebersole 1980) based on experimental manipulation of food supply. In coho salmon the distance from which an intruder is attacked is an increasing function of short-term hunger (Dill et al. 1981), a phenomenon which would produce the observed inverse relationship between food availability and territory size, and maximize the fish's net rate of energy intake.

Although increased feeding rate, diet breadth, and territory size with increasing hunger are evidently adaptive, the question can just as easily be framed in reverse; i.e. is it adaptive for feeding rate and aggressive behavior to decrease as satiation nears? Because it is likely that high activity levels increase vulnerability to predation, decreased foraging activity may be viewed as an adaptive response to predation risk. This question is considered in a later section. Assimilation efficiency, and thus net energy value of prey, may also decrease as satiation nears (Elliott 1976), and this could also make a decreased feeding rate adaptive.

Threat of Competition

If, as argued in the last section, defense of a feeding territory can be viewed as a part of some fishes' foraging strategy, then there should be an optimal amount of aggressive behavior, one which ensures that the cost of defense does not outweigh the benefits gained thereby. All intruders on a territory do not represent equivalent degrees of threat to the food resource of the territorial resident. The benefits gained by their expulsion are therefore not equal; nor will be the optimal expenditures on defense. It would therefore be adaptive if the aggressiveness of a resident were in some way "scaled" to the degree of threat posed by a particular intruder, and there is considerable evidence suggesting that this is indeed the case.

Damselfishes (Pomacentridae) have been especially well studied in this regard. Although their territories are undoubtedly multifunctional, providing food, shelter, and nesting sites, most of a pomacentrid's food is produced within its territory. Using what he calls the "model bottle" technique (an intruder is placed in a glass jar and moved in steps successively closer to the center of a territory), Thresher (1976) has shown that the threespot damselfish (*Eupomacentrus planifrons*) defends the largest territories against those species which feed on the same benthic algae as itself, and that

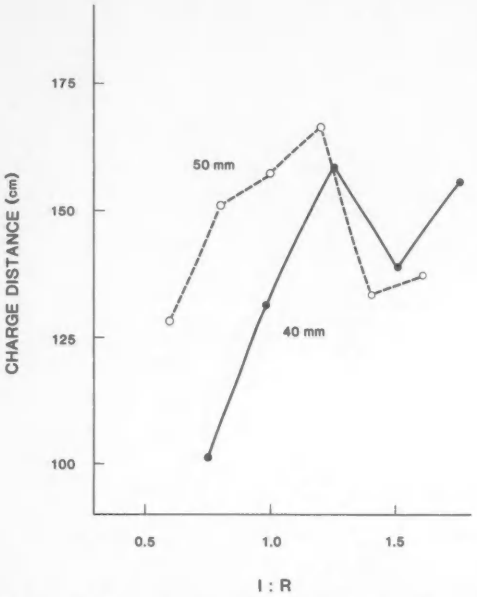

FIG. 1. The effect of model intruder:resident size ratio (I:R) on charge distance of resident 40- and 50-mm coho salmon juveniles.

territory size correlates significantly with the amount of algae in the diet of each intruder species. Such "serial territoriality" (different defense radii for different species of intruder) has also been documented in the laboratory (Patterson 1975; Thresher 1978).

Ebersole (1977) has shown in a related species, the Beau Gregory (*E. leucosticus*), that the degree of aggression shown towards an intruder is highly correlated with its potential competitive impact (diet overlap multiplied by relative metabolic demand). Because metabolic rate is a power function of body size, one would expect there to be a relationship between aggressiveness and intruder size for conspecific intruders as well; I will return to this point later.

A number of other aspects of the territorial defense system of Pomacentrids appear to be adaptive in energetic terms. *Eupomacentrus planifrons* distinguish between neighbors and strange conspecifics in model bottle tests, attacking the latter at greater distances (Thresher 1979), and have the greatest threat distance when on their preferred staghorn coral substrate (Itzkowitz 1979). Neighboring territory holders presumably represent less threat to the food supply, and preferred substrate is more worth defending. Finally, *E. fasciolatus* learn to attack novel intruders (tilapia) after seeing them grazing just outside the territory (Losey 1981).

As noted above the size of a conspecific should be an indication of the degree of threat it poses to a territory resident's resources, not only because of increased metabolic demand with increasing size, but also because of shifts in diet with growth. Thus both interspecific and intraspecific territoriality might be expected to be "serial" with intruder size, the largest territories being defended against that size posing the greatest threat. Pomacentrids have been examined in this regard but the evidence is equivocal. Patterson (1975) concludes that territory size in juvenile *E. planifrons* depends on the size of the intruder, but her data are very limited. Using the same species Myrberg and Thresher (1974) showed that small *Holacanthus tricolor* were attacked at a significantly shorter distance than larger ones, but there was no such effect in a second intruder species. The anemonefish *Amphiprion melanopus* does attack small juveniles at shorter distances and with less intensity than larger adults, but Ross (1978) does not consider these fish to be defending feeding territories.

We have attempted to examine this question in juvenile coho salmon. This species defends feeding territories in streams and, owing to variable emergence times and growth rates, and to the presence of two year-classes in the stream at certain times, residents are faced with the possibility of intrusions by individuals of a wide range of sizes. As the diet (characterized by prey size) of coho changes with body size (R. L. Dunbrack unpublished data), threat of competition will not be constant. In fact, competitive impact will be potentially most severe when the intruder is slightly larger than the resident (Wilson 1975), because large intruders still eat many of the prey sizes consumed by the smaller resident and, moreover, eat more of them. Attack distance should therefore also be greatest to intruders slightly larger than the territory holder itself.

To test this hypothesis we presented juvenile coho resident in small aquaria with model intruders moved at intervals toward them, and recorded their attack (charge) distances. Details of the general experimental procedure are provided in Dill et al. (1981). The residents were either 40 mm ($n = 27$) or 50 mm ($n = 22$) fork length. The model intruders ranged from 30 to 70 and 30 to 80 mm, respectively, in increments of 10 mm. They were blowups to various size of a single color photograph of a coho salmon. Each resident was tested with each intruder size, in random order, and fed one brine shrimp between trials. Figure 1 shows the mean charge distances for each size of resident as a function of the intruder–resident size ratio (e.g. the response of a 50-mm resident to a 70-mm intruder is plotted at I:R 1.4). For each resident size, charge distance was maximal when the intruder was 25–30% larger than the resident. The decline above this size is significant for 50-mm residents (one-tailed t-test, $P < 0.05$ for both 70- and 80-mm intruders), but not for 40-mm residents. Nevertheless, it is apparent that charge distance is a continually increasing function of intruder size only if model intruders (Fig. 1) and live intruders (Dill 1978b) are smaller than the resident. Thus charge distance is adaptively, if imperfectly, scaled to the threat of competition.

We have not determined whether the intensity of aggression in coho is related to threat of competition in the same way, although charge velocity is an increasing function of intruder size for small intruders (Dill 1978b). It would not be surprising to find such scaling in this measure of aggression, although Thresher (1978) has demonstrated that the mechanisms underlying distance of attack and vigor of attack are causally independent in three-spot damselfish.

Wańkowski and Thorpe (1979) reported that the greater the difference in length between dominant and subordinate Atlan-

tic salmon (*Salmo salar*), the fewer the bouts of fighting which occur; less fighting is also seen among subordinates when there is greater length variation within the group. The behavioral mechanism is uncertain, but these findings are also explicable as a result of the scaling of aggression to threat of competition (although risk of injury from fighting could be invoked as an alternate explanation). The importance of aggressive scaling in the field is uncertain, as many salmonids have a tendency to move to deeper and faster water as they grow, resulting in a certain amount of habitat segregation by size (Chapman and Bjornn 1969; Smith and Li 1983; Wańkowski and Thorpe 1979). Attack distances of salmonids to other species of about the same size (e.g. coho vs. steelhead) have not been examined, but might repay study given the work on damselfish discussed earlier.

Risk of Predation

Foraging has potential costs associated with it other than the expenditure of energy and time; the most obvious of these is risk of predation. Because many predators are simultaneously prey of animals higher on the trophic scale, a foraging behavior would be expected to strike an adaptive balance between energetic return and risk. However, foraging strategy models seldom consider risk of predation, primarily because energy and risk cannot be expressed in the same units, or "currency," and simple models with soluble optima therefore cannot be constructed. Unlike many areas of ecology, this is one field in which theory lags behind data: there have been several empirical demonstrations that animals, including fishes, respond to risk of predation by modifying their foraging behavior in ways which appear to be adaptive.

Some habitat patches may be energetically rewarding but harbor dangerous predators. If fishes are faced with a choice between such a patch and one both less rewarding and less dangerous, their decision should reflect both the degree of risk involved, and the relative energetic advantage (Sih 1980). Foraging behavior in bluegill sunfish (*Lepomis macrochirus*) is consistent with this prediction (Mittelbach 1981). Large bluegill (>100 mm) shift from the vegetated littoral zone to the open water of lakes at a time in nearly complete accordance with predictions for maximizing net energetic intake. Although smaller size-classes should switch at the same time, they do not, but instead continue to use the vegetated habitat. This reduces their energetic return but presumably minimizes their chances of being eaten by largemouth bass (*Micropterus salmoides*) in open water. Large bluegill are less vulnerable to this predator. In a pond without predators, even small bluegill forage in the habitat best from the standpoint of energetic return (Werner and Mittlebach 1981). Although not collected for this purpose, the observation of Kramer et al. (1983) that many species of fish respond to an aerial predator by increasing their mean depth in the water column suggests that surface-feeders might also reduce risk at the cost of foraging efficiency.

Differences in risk between habitats may be more subtle than this. Schools or swarms of prey may provide good feeding opportunities but, because of a "confusion" effect, interfere with a forager's ability to detect the approach of a predator. Milinski and Heller (1978) have shown that the threespine stickleback's choice of *Daphnia* swarm density can be altered by exposure to a model of an avian predator (a kingfisher). Prior to exposure hungry fish choose the high density swarm, where their feeding rate is highest (Heller and Milinski 1979); after exposure to the model, they attack swarm regions of lower density. Although this decreases feeding rate, it may increase ability to detect predators. Partially satiated sticklebacks actually feed at the highest rates in the lowest swarm densities, being either unwilling or unable to feed efficiently at high densities (Heller and Milinski 1979). This observation suggests a trade-off between energetic return and risk which varies as a function of the energetic need (hunger) of the fish.

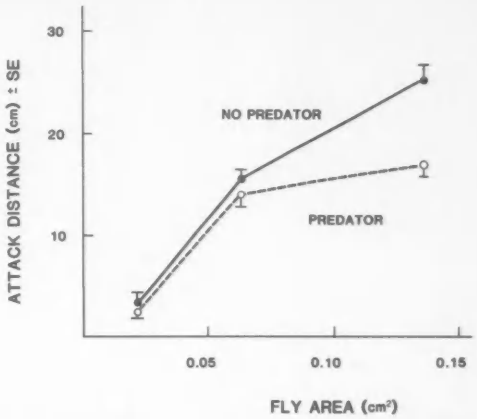

FIG. 2. The effect of the presentation of a model predator (rainbow trout) on the distance swum to attack flies of different size (length × width) by juvenile coho salmon. Only the reduction for the largest fly size is significant ($P < 0.001$).

Empirical demonstrations to date of predator risk–sensitivity have dealt with patch utilization. Little attention has been given to the possibility that risk of predation may alter the choice of diet items by a forager within a given habitat. We are beginning to explore this issue in juvenile coho salmon. The size-distribution of drifting prey in a juvenile coho's diet can be accurately predicted from knowledge of the relative abundance of different prey size-classes and the fish's reactive distance for each prey size (Dunbrack and Dill 1983). Reactive distance is an increasing, but decelerating, function of prey size. Upon detecting a prey item the fish swims upstream from its holding station to intercept it, and the distance swum (attack distance) is less than, but highly correlated with, reactive distance. Although cryptic when stationary, the coho presumably becomes more visible, and hence more vulnerable, to predators during these feeding excursions. Consequently, prey size and predation risk are associated variables, and we hypothesize that the fish will swim shorter distances for a given prey item when it perceives risk to be high.

We tested this hypothesis by measuring the attack distance of twelve 70- to 73-mm fork length coho in response to three sizes of surface-drifting flies in the artificial stream channel

TABLE 2. Effects of experience on fish foraging behavior.

Behavior affected	Species	Source
1. *Searching increases*		
Response to prey odor	Yellowfin tuna	Atema et al. (1980)
Reactive distance	Threespine stickleback	Beukema (1968)
Reactive distance	Rainbow trout	Ware (1981b)
Path efficiency	*Caranx melampygus*	Potts (1980)
2. *Attack latency decreases*	Pink salmon (*Oncorhynchus gorbuscha*)	Godin (1978)
3. *Capture success increases*	Tiger musky (*Esox* hybrid)	Webb and Skadsen (1980)
	Sacramento perch (*Archoplites interruptus*)	Vinyard (1982)

described by Dunbrack and Dill (1983). Predation "risk" was manipulated by presenting fish singly with a photograph of a 20-cm rainbow trout. This model predator was moved forward into the coho's field of view, and then backward behind a screen, at intervals of about 21 min with the aid of pulleys, an electric motor, and a timing device. In another 12 trials the same fish received no such stimulus. Whether the predator or no-predator trial occurred first was determined randomly for each fish. In all trials the fish was presented with three of each size of fly, in random order. Attack distances (Fig. 2) were reduced in the presence of the model predator, particularly in response to the largest prey ($t = 4.79$, $P < 0.001$). We have subsequently shown that this response of decreasing attack distance is specific to a fish-like object (it is not shown when the object is a black rectangle of the same size), is more marked the higher the predator presentation frequency, and is less marked the hungrier the fish. These experiments, to be reported in detail elsewhere (L. M. Dill and A. H. G. Fraser unpublished data), again suggest a quantitative trade-off between risk and energetic demand. As the reduction in attack distance is only significant for larger prey, the effect should be to reduce the relative proportion of large prey in the diet, reducing the rate of energy intake, and consequently the growth rate (this can be thought of as an example of behavioral resource depression, Charnov et al. 1976). Whereas fitness is likely to be decreased as a result of the reduced growth rate (Dill 1978a), this may be compensated for by a reduced rate of predation.

Despite such empirical evidence that fish do trade-off risk of predation and foraging efficiency, it is not yet possible to include such considerations in foraging models because, as mentioned earlier, these factors have not yet been measured in comparable units. Two solutions to this dilemma are possible. First, the animal could be presented with a variety of combinations of risk and energetic reward, and its choices observed. The amount of risk the animal is willing to accept for a given increase in energetic reward (or, conversely, the energy it will forego for a given reduction of risk) should provide us with the weightings of these two factors used by the animal itself. In effect, the fish could tell us how to express the two factors in a common currency. This is the approach we are adopting in our ongoing studies. Alternatively, the effects of both risk and energy intake on some direct measure of fitness can be estimated. An appropriate measure would be expected lifetime reproductive output, which integrates age-specific fecundity (size- and thus growth rate-dependent) and age-specific mortality. This approach is being adopted in further studies of habitat choice in sunfish (E. E. Werner personal communication).

The Role of Experience

Learning, defined most simply as a change in behavior with experience, is an important mechanism of adaptation to environmental unpredictability. By means of it, fish can fine-tune a generalized foraging pattern to the current environmental situation, increasing their foraging efficiency by developing behaviors appropriate to the currently most abundant prey, or by learning to avoid prey difficult to catch or handle (Vinyard 1980; Ohguchi 1981).

Well-documented effects of experience on foraging behavior of fishes are listed in Table 2 (I have not included several effects reported for larval fishes, as these may have resulted from maturational processes). One obvious consequence of these changes will be an increased capture rate with experience of a prey type, as shown by Werner et al. (1981) for bluegill sunfish feeding on *Daphnia* or *Chironomus* larvae; in the latter case the increase with experience was about fourfold. Ringler (1979) has similarly documented an increase in attack rate with experience in drift-feeding brown trout (*Salmo trutta*). Not only will a prey type be captured more rapidly but its profitability value will increase with experience: net energetic value will increase and handling time will decrease as a result of changes in both attack latency and capture efficiency (less time, and thus energy, will be required for each successful attack).

The net energy value of a prey type could also be altered in another way as a result of experience with it. If experience results in a physiological change, such as in the relative proportions of various digestive enzymes, the assimilation efficiency for a particular prey type will rise, increasing its net worth. This possibility has been suggested by workers on several animal groups (Milinski and Loewenstein 1980; Partridge 1981) but has not been documented in fishes. It remains an interesting possibility worthy of experimental investigation.

A predator should find it energetically advantageous to specialize on the most profitable prey (type 1) whenever its net energy return will be greater by doing so than by broadening its diet to include the next most profitable prey (type 2). This can be stated in the form of the following inequality (Krebs and Davies 1981): it is energetically advantageous to specialize on prey type 1 if

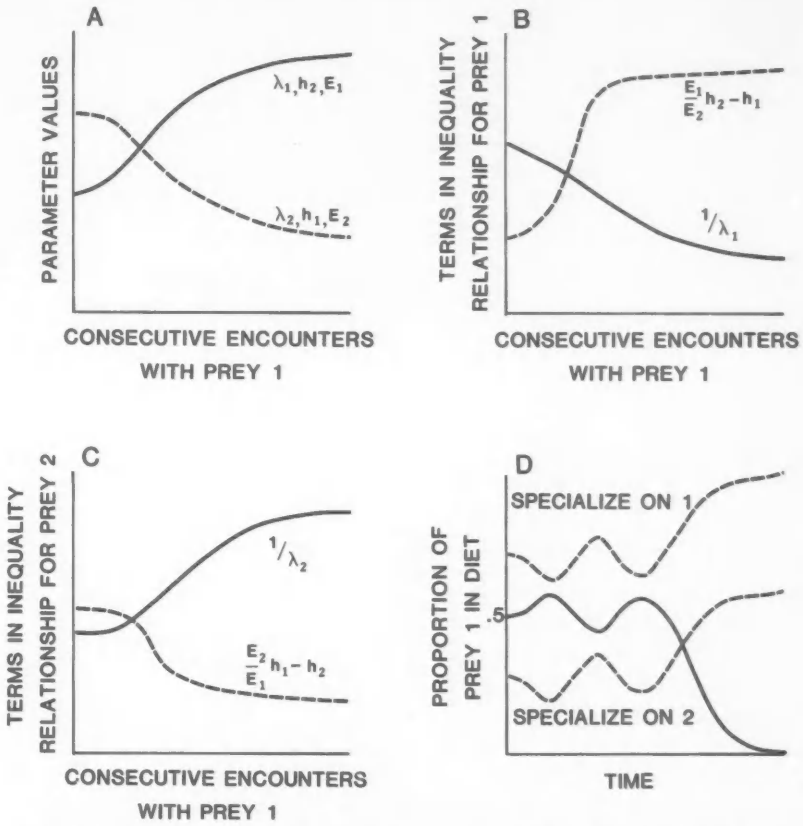

FIG. 3. Graphical analysis of the effect of experience on prey preference. (A) The effect of consecutive encounters with prey type 1 on encounter rates (λ_i), net energy values (E_i), and handling times (h_i) for two prey types. Learning is assumed to be antagonistic and although prey 2 is initially the most profitable ($E_2/h_2 > E_1/h_1$), this is reversed after a number of consecutive encounters with prey 1. (B) The effect of these changes on the terms in inequality (12). Once $1/\lambda_1$ falls below the dotted line, specialization on prey 1 is predicted. (C) The equivalent terms for prey 2. Specialization on this prey becomes increasingly unlikely after several consecutive encounters with prey 1. (D) The hypothesized effect of random sampling on the likelihood of diet specialization. The two prey are assumed to be of equal abundance and profitability initially, but at any point in time the proportions of the two types in the diet will deviate from perfect equality. The boundaries represent the proportions of prey 1 in the diet (p_1) required to cause $1/\lambda_1$ to fall below $(E_1/E_2)h_2 - h_1$ (upper dotted line) or $1/\lambda_2$ below $(E_2/E_1)h_1 - h_2$ (lower). These change in parallel, but in antiphase and phase with p_1, respectively (compare [B] and [C] above). In this example, chance crossing of the lower boundary results in specialization on prey type 2, but specialization on type 1 is equally likely. Once specialization has occurred a large change in relative availability would be required to cause switching to the alternate prey. The number of individuals likely to specialize on each of two prey types will depend on the initial differences in abundance and profitability of the two prey, and on the fish's sampling procedure.

$$(12)\quad 1/\lambda_1 < \frac{E_1}{E_2}h_2 - h_1$$

where E_1 and h_1 are the net energy values and handling times of the two prey types, and λ_1 is the encounter rate with prey 1 ($1/\lambda_1$ is the average time between encounters with this most preferred prey). Notice that the value of every parameter in this inequality can be modified through experience of a particular prey type.

The fact that prey will be captured at an increasing rate (up to some asymptote determined by the predator's learning capability), while their profitability increases simultaneously,

lends an element of positive feedback to the system; a preferred prey will become even more so. The simultaneous increases in λ_1 and E_1, and the decrease in h_1, mean that once a fish has begun feeding on prey type 1, there is an increasing likelihood that the inequality will hold and the animal will find it profitable to continue to specialize on this prey type. If learning is antagonistic in any sense, e.g. if developing an ability to handle one type of prey reduces the ability to handle other types, experience with prey type 1 will reduce the profitability of type 2, and further drive the animal towards specialization. These effects are summarized in Fig. 3A–C with reference to the inequality equation.

This mechanism can produce the phenomenon of "training bias," the tendency for an animal to prefer the food type which it has eaten most recently. Training bias for familiar foods has been reported in rainbow trout (Bryan 1973), chum salmon fry *Oncorhynchus keta* (LeBrasseur 1969), and threespine sticklebacks (Meesters 1940; Milinski and Loewenstein 1980). This training bias can be an important factor leading to dietary differences between individuals in a population, even when they are exposed to the same prey spectrum in a single habitat. The random element involved in initial sampling of a habitat is of critical importance. A few consecutive encounters with a particular type of prey (a finite possibility even if the prey is rare) can so alter the parameters of the inequality that specialization on this prey becomes optimal (Fig. 3D). However, such specialization may not be globally optimal. The fish might have done better by specializing on a different prey type initially, but (to use current jargon) finds itself trapped on a local peak in the adaptive landscape; to reach a higher neighboring peak requires traversing a valley bottom and sacrificing short-term foraging efficiency. It is unlikely, however, that the heights of these adaptive peaks could be vastly different. If they were, the local optimum would probably be unstable, and all fish would tend toward the global optimum over time.

Individual diet specialization is a fairly common phenomenon in fish, being reported in brook trout, *Salvelinus fontinalis* (Allan 1981), brook, rainbow, and cutthroat trout (*Salmo clarki*) (Bryan and Larkin 1972), and larval herring, *Clupea harengus* (Rosenthal and Hempel 1970). Werner et al. (1981) observed that individual bluegill sunfish tended to specialize on either benthos or plankton, achieving about the same return rates in the two habitats. Both types of specialist did better (in terms of prey items per stomach) than the generalists. Similarly, Bryan and Larkin (1972) found no effect of degree of specialization on feeding or growth rates. Thus, available evidence suggests that different types of specialist do equally well, i.e. that the adaptive peaks are of nearly equal height. However, the possibility remains that specialization can at times be maladaptive, particularly in situations in which the least profitable prey is also the most abundant.

It is worth pointing out that although several of the effects of experience on foraging (Table 2) are similar to those of hunger (Table 1), diet specialization may result in the former case, and diet generalization in the latter. This is entirely due to the fact that only experience has well documented effects on encounter rate (λ_1), and that only the E and h terms for prey 1 are affected by learning.

The possible role of experience in producing training bias and diet specialization has not escaped the attention of other workers. Hughes (1979) modeled a situation in which handling time (or attack success rate) is a function of encounter rate with a prey type (i.e. dependent on λ_1). Under this assumption, prey types may be transposed in profitability rank as a result of learning, and it may become optimal to specialize on an abundant prey, even if it is initially the less profitable type. This violates a general conclusion from optimal foraging theory (Pyke et al. 1977), which states that a less-preferred prey cannot become preferred by virtue of becoming more abundant. McNair (1981) reached similar conclusions using a slightly different model (the ability to see, capture, and/or handle prey is dependent upon the relative abundance of prey types; for ability to see, this is true even if some prey are not attacked). McNair (1979) pointed out that any tendency for the type of prey last encountered to influence the type of prey next encountered will have the same effect. This will occur, for instance, if search is concentrated in the vicinity of a capture ("area restricted searching"), as shown in larval herring (Rosenthal and Hempel 1970), larval anchovy (*Engraulis mordax*) (Hunter and Thomas 1974), and threespine sticklebacks (Thomas 1974). Conversely, after rejecting a prey, sticklebacks swim faster and along a straighter path than previously, apparently showing "area avoided searching" (Thomas 1974). These behaviors will speed up any learning process and increase the chances of specialization. Werner et al. (1981) discussed the role of learning in a fish's decision as to which habitat to forage in, pointing out that profitability of alternative habitats may be underestimated by naive fish, resulting in lags in switching to the best patch. This will obviously be important in the context of prey choice as well, as a novel prey will initially have low profitability, requiring a substantial increase in abundance before the fish switches its attention to it. In both diet and habitat choice situations, the predator may not behave optimally in the short term.

Concluding Remarks

In this brief, and by no means comprehensive, review of their foraging behavior, I hope to have demonstrated that fishes possess the ability to alter their behavior appropriately in response to variations in such factors as food availability, threat of competition, risk of predation, and experience. The main point is that fish foraging behavior is characterized by adaptive flexibility.

Flexibility in response to varying food availability is not surprising; this is one type of environmental change concerning which optimal foraging theory makes a precise prediction. Accordingly, my emphasis was on behavioral mechanisms; hunger was proposed as an appropriate motivational system linking food availability and predatory behavior in a way which ensures that fish alter their behavior in an adaptive fashion. The scaling of aggressive behavior to degree of competitive threat is also predictable from current foraging theory, if the theory is extended to consider aggression and territorial defense as part of an animal's foraging strategy.

In the case of predation risk, the empirical evidence presented begs reassessment of the optimality criterion assumed by most current foraging models. It is clear that at least fishes (and in all likelihood most animals) are optimizing a

function much more complex than energy intake rate alone. Risk of predation will have to be included explicitly in future generations of models, although doing so presents some formidable practical problems. The lack of realism of current models is also emphasized by the failure of most of them to consider dynamic changes in the behavior of animals mediated by learning. Certain important conclusions of present models are no longer valid once learning processes are included.

I am of the opinion that the application of current optimality models of foraging has reached a stage of diminishing returns. Many recent papers either make only minor modifications to the theoretical structure, or test it on yet another species, providing no new insights. Papers titled "Optimal foraging by species X" are not vastly different in terms of their contribution to understanding than those titled "Food of species Y in lake Z."

Although I have criticized the realism and applicability of current foraging models, I remain a believer in the usefulness of optimality models in behavior. I am optimistic that future generations of foraging models will improve considerably on current ones, applying techniques such as dynamic optimization, which allows explicit consideration of feedbacks and trade-offs (Krebs et al. 1981). Hopefully, these modeling efforts will be based upon empirical research on behavioral mechanisms and capabilities, and will be experimentally verified at each step, lest the theory again outstrip the data. In the meantime, it is not unreasonable to claim that fish are more sophisticated than models (and modelers).

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Analysis of the Biological and Demographic Parameters of Northern Sand Lance, *Ammodytes dubius*, from the Newfoundland Grand Bank

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WINTERS, G. H. 1983. Analysis of the biological and demographic parameters of the northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank. Can. J. Fish. Aquat. Sci. 40: 409–419.

Biological characteristics and population dynamics of northern sand lance (*Ammodytes dubius*) population on the Grand Banks were investigated in the period 1968–79. Sand lance were distributed mainly in the shallower areas of the Grand Banks, particularly in the northeast and southeast areas. Through an examination of reproduction parameters I conclude that spawning occurs principally during the period November–January. Growth rates of Grand Bank sand lance are within the range of those described for the Scotian Shelf and are well correlated with temperature variations. Abundance indices, derived from groundfish surveys, indicate a substantial increase in abundance since the 1960s, and this increase is attributable to increased recruitment and reduced natural mortality. From correlation analyses I suggest that the decline in the Grand Bank population of Atlantic cod (*Gadus morhua*) may be responsible for the reduced mortality rates and increased abundance of Grand Bank sand lance during the 1970s.

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Les caractéristiques biologiques et la dynamique de la population de capelans (*Ammodytes dubius*) du Grand banc ont été étudiées pendant la période de 1968 à 1979. L'espèce est répartie surtout dans les régions peu profondes du Grand banc, en particulier celles du nord-est et du sud-est. Un examen des paramètres de reproduction me permet de conclure que la ponte a lieu principalement de novembre à janvier. Les taux de croissance du lançon du Grand banc se comparent à ceux de la population du plateau Scotian et sont étroitement liés aux variations de température. Les indices d'abondance, déduits des relevés de poissons de fond, indiquent une substantielle augmentation de l'effectif depuis les années 1960, augmentation attribuable à un recrutement accru et à une mortalité naturelle réduite. À la lumière d'analyses de corrélations, j'avance l'hypothèse que le déclin de la population de morues (*Gadus morhua*) du Grand banc serait responsable de la diminution des taux de mortalité et de l'augmentation de l'abondance du capelan du Grand banc pendant les années 1970.

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SAND lance (*Ammodytes* spp.) are small semidemersal fish which range extensively in the Northwest Atlantic from Cape Hatteras, N.C. to West Greenland (Leim and Scott 1966). They sometimes form large schools and are usually abundant in areas where the bottom substrate consists of sand and fine gravel particularly on the southeast shoal of the Grand Bank (Fig. 1) where they mix extensively with capelin (*Mallotus villosus*) during the capelin spawning season in that area. Sand lance are also similar to capelin in their role as important fodder species in the Northwest Atlantic and fill a strategic niche in the marine ecosystem, acting as an important trophic link between zooplankton and a variety of piscivorous marine vertebrates (Reay 1970). Indeed their size and shape render them ideal food items for most predators. *Ammodytes dubius* is the single most important prey species of American plaice (*Hippoglossoides platessoides*) comprising nearly 80% of the food spectrum of that species in the southern Grand Banks area (Pitt 1973). Sand lance also contribute to the diet of yellowtail flounder (*Limanda ferruginea*) on the Grand Bank (Pitt 1976) although not to such a substantial degree as in American plaice. In addition sand lance form the dominant prey species of cod in the southern Grand Bank area (Popova 1962) and are also important in the diet of cod in the northern Grand Bank area (Turuk 1968).

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Sand lance are also an important prey species in other areas of the Northwest Atlantic. In the West Greenland area Atlantic salmon feed extensively on sand lance (Templeman 1966; Lear 1980) as well as around coastal Newfoundland waters (Lear 1972). On the Nova Scotian Shelf, Atlantic cod, (*Gadus morhua*) American plaice, silver hake (*Merluccius bilinearis*), and haddock (*Melanogrammus aeglefinus*) feed extensively on sand lance (Scott 1968, 1973), and a similar predator–prey interaction occurs on the American continental shelf area (Bowman and Langton 1978). In addition such large marine mammals as fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeanglia*) whales feed heavily on sand lance (Overholtz and Nicolas 1979).

There is a paucity of published information on the ecology and population dynamics of sand lance in the Northwest Atlantic in general and on the Newfoundland Grand Bank in particular. Meristic and morphometric studies have been reported by Winters (1970) and Scott (1972) and larval and post-larval data have been documented by Dannevig (1918) and Frost (1938). The only information available on the vital parameters of Grand Bank sand lance is an analysis of their growth patterns from back-calculations based on otoliths (Winters 1981). Given the substantial attrition in the biomass of cod and flounder on the Grand Bank during the 1970s (Anon. 1980) and the recent substantial reduction in capelin abundance (Anon. 1980), the role of sand lance in the ecology of the Grand Bank has probably been greatly altered. This paper examines the available historical data on sand lance from the Newfoundland Grand Bank and presents new information on the recent demography of this stock.

Materials and Methods

Random samples of sand lance from various areas of Grand Bank were obtained from incidental catches of that species by research vessels of the Department of Fisheries and Oceans during the period 1968–79. Standard trawling gear consisted of a No. 36 or No. 41.5 Yankee bottom trawl with a codend liner of mesh size ranging from 15 to 30 mm; a standard tow was of 30 min duration. Specimens were examined in detail after preservation in frozen brine. Lengths represent total lengths as measured from the tip of the mandible to the ventral lobe of the caudal fin, deflected backwards in a straight line with the body. Conversion of thawed lengths to fresh equivalents was derived from regression analysis of several samples of lance measured fresh and after thawing, indicating a conversion factor of 1.03.

Age determinations were based on otolith interpretations according to the methodology of Macer (1966) and Scott (1968, 1973). Otoliths with poorly defined annuli (about 5% of the total sample) were omitted in age determinations. However, age-group determinations beyond age 6 probably contain significant error due to poorly defined annuli at the margins of otoliths in older specimens.

Gonad development and stage of maturity were classified according to the following stages; 0, immature; 1, maturing (developing); 2, ripe; 3, running; 4, spent; and 5, recovering. Specimens were assigned to these categories according to gonad condition as described by Macer (1966).

Results

Distribution Patterns

The relative abundance of sand lance as derived from bottom-trawl surveys of the R.V. *A. T. Cameron* during the period 1959–80 are shown in Fig. 2. The highest densities (Fig. 2) of sand lance from 1959 to 1980 occurred on top of the Bank with abundance levels decreasing towards the slopes. Sand lance appear to be most abundant in the eastern half of the Grand Bank, particularly in the northeast portion and around the Southeast Shoal area. These areas also have sedimentary facies which are predominantly comprised of sand and fine gravel (Sen Gupta and McMullen 1969) whereas the western edge of Grand Bank which has a relatively low abundance of sand lance is mainly an area of rocky bottom.

Table 1 illustrates seasonal changes in the catchability of sand lance in three NAFO Divisions. There are two periods of high availability of sand lance, during the late spring (April–June) and in early fall. The short period of high availability during early fall may be due to the shift in the distribution of sand lance at this time of the year to deeper cooler water which may tend to concentrate local populations of sand lance.

Although having a wide depth distribution to depths in excess of 270 m, sand lance on the Newfoundland Grand Bank are mainly concentrated in the shallower waters on top of the bank where depths are generally less than 100 m (Fig. 3). They also tend to prefer cold water, being abundant mainly in the temperature range of −1 to +2°C. Scott (1968), however, concluded that *A. dubius* over the Nova Scotian banks was eurythermal with fish being taken from waters ranging from −2 to 11°C, although the largest catches were from waters with temperatures between 3 and 6°C.

A progressive movement of sand lance to deeper water during the summer period, followed by a return to shallower depths during the fall, is indicated (Fig. 4A). The summer migration into deeper water is also associated with warmer temperatures (Fig. 4B) until September–October when temperature preferences suddenly drop until late fall when warmer temperatures again prevail, perhaps in response to the physiological requirements of tertiary gonad development prior to spawning.

Age Composition Analysis

Age composition data of mature sand lance from the Grand Bank for the period 1968–79 are shown in Table 2. The data indicate a change in population age structure beginning in 1975 when 3-yr-olds began to be the dominant age-group compared with 4-yr-olds prior to 1975. A comparison of the relative abundance of age-group 3 in the samples suggests that the 1968 year-class was relatively strong but that since the 1972 year-class recruited to the adult stock in 1975, recruitment has been steadily increasing during the late 1970s. Concomitant with this apparent increase in recruitment in the late 1970s is a greater predominance of older age-groups (age-groups 7+) suggesting perhaps improved survival of all age-groups during the mid 1970s.

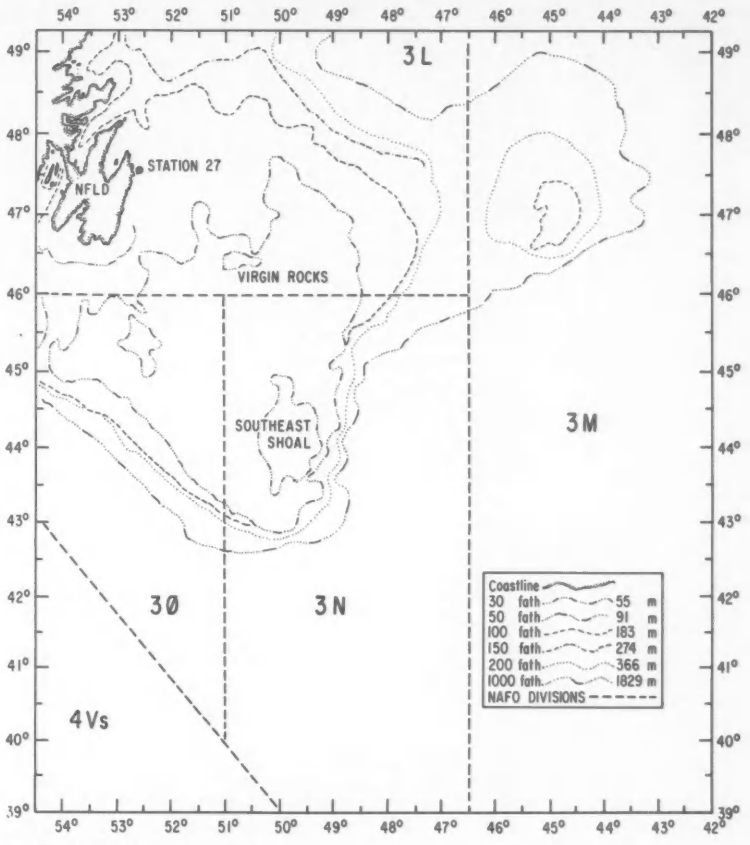

FIG. 1. Localities mentioned in the text.

The maximum life span (at least 10 yr) recorded here for specimens of *A. dubius* from Grand Bank is greater than that documented for the Scotian Shelf (Scott 1968, 1973) and the North Sea (Macer 1966) for sand lance. This is consistent with the slower growth rate of Grand Bank sand lance compared with those from Emerald Bank (Winters 1981) but may also reflect the fact that the Scotian Shelf age samples were taken during the late 1960s and early 1970s when groundfish abundance in that area was relatively high resulting in high predation rates of sand lance and thereby reduced survival rates to the older age-groups.

GROWTH PARAMETERS

A comparison of mean lengths-at-age of mature sand lance during the period 1969–79 (Table 3) indicates relative stability in this character during the time interval involved. The relative growth coefficient defined as

$$RCG = \Sigma (L_{t+1} - L_t)/L_t$$

was also calculated for those age-groups (2–6) which would be least affected by aging inconsistencies. This growth parameter for Grand Bank sand lance has shown major fluctuations during the period under consideration, although without apparent trend.

Examination of the length–weight relationship from samples of sand lance during the second quarter indicates an adherence to the isometric growth law (Fig. 5).

The age–weight relationship of Grand Bank sand lance (Fig. 6) is approximately sigmoidal. The younger ages (1–3) may be biased upwards as a result of probable trawl selectivity in the lower length ranges.

REPRODUCTIVE PARAMETERS

Maturity ogives of Grand Bank sand lance (Fig. 7) indicate a mean age of maturity of ~3 yr and a mean length at maturity of 180 mm.

Gonad development is relatively slow during the spring–summer period and it is not until the September–October

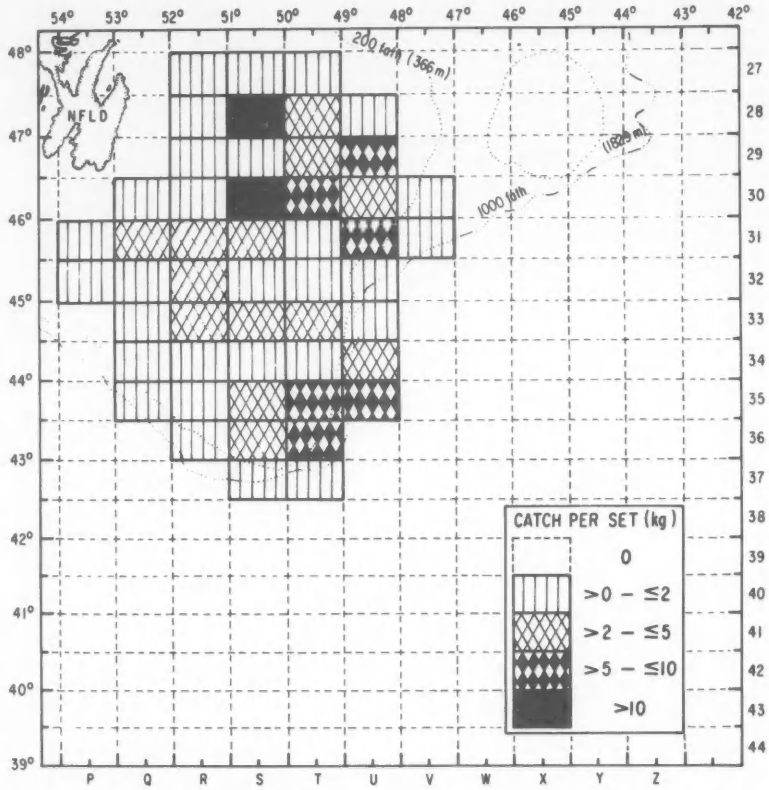

FIG. 2. Relative abundance (kg/set) of sand lance on the Grand Bank as derived from bottom trawl surveys of the *A.T. Cameron* 1959–80.

TABLE 1. Catch per successful set in NAFO Divisions 3L, 3N, and 30 by the *A.T. Cameron*, 1959–80. The number of sets are included in parentheses.

Month	Catch/successful set (kg)			
	3L	3N	30	3LNO
January	—	≤0.1 (2)	—	≤0.1 (2)
February	—	—	—	—
March	—	≤0.1 (2)	—	≤0.1 (2)
April	0.1 (4)	5.5 (66)	5.7 (25)	5.3 (95)
May	9.4 (94)	6.7 (87)	9.0 (37)	8.2 (218)
June	16.7 (27)	6.4 (100)	6.7 (69)	7.9 (196)
July	0.3 (8)	3.2 (25)	0.6 (13)	2.0 (46)
August	1.0 (8)	1.9 (10)	—	1.5 (18)
September	≤0.1 (2)	0.9 (14)	—	0.8 (16)
October	22.3 (26)	4.6 (85)	—	8.5 (111)
November	—	0.3 (8)	—	0.3 (8)
December	—	0.3 (1)	0.2 (6)	0.3 (7)

period that a significant progression through the maturity stages occurs (Fig. 8). This is supported by a rapid development of the gonads between July and October (Fig. 9). Taken together these data suggest that the main spawning season of sand lance on the Grand Bank occurs during the period November–January. This is further supported by catches of recently hatched larvae in early March by Soviet surveys in the Grand Bank area (Serebryokov 1962). Scott (1968) identified a similar well-defined winter spawning season for *A. dubius* from the Scotian Shelf area. However, the presence of spent fish in April and May (Fig. 8) indicates that minor peaks in spawning may occur in late winter.

ABUNDANCE INDICES

Annual groundfish surveys of the Grand Bank (NAFO Div. 3LNO) have been carried out by the R.V. *A. T. Cameron* since 1959. Prior to 1971 these surveys were mainly based on line transect methodology whereas since 1971 additional surveys based on a dedicated random-stratified sampling design have been conducted. The general trend from the dedicated surveys is for a cycling upwards in abundance of sand lance since 1971 and particularly since the mid-1970s (Fig. 10).

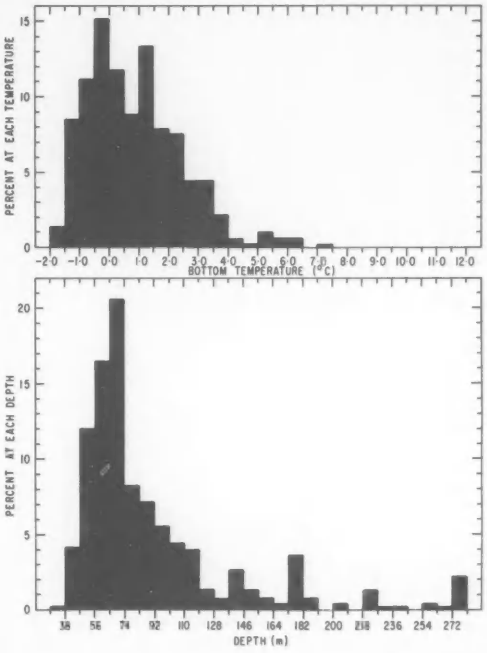

FIG. 3. Distribution of sand lance on the Grand Bank in relation to depth and temperature as derived from survey data for the period 1959–80.

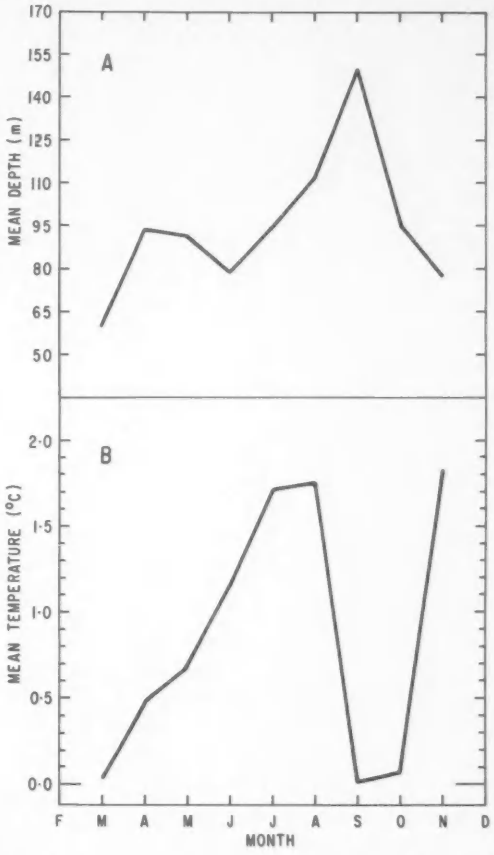

FIG. 4. Seasonal pattern of depth and temperature distribution of sand lance on the Newfoundland Grand Bank.

Abundance of sand lance as determined from the combination of all groundfish surveys was relatively stable at a low level up to the late 1960s and has gradually increased since then to current levels which are several times higher than comparable abundance indices during the 1960s (Fig. 11). A similar magnitude of increase in sand lance abundance has been documented for the area from Cape Hatteras to the Gulf of Maine (Meyer et al. 1979) although the temporal pattern is somewhat different in that sand lance populations in those areas were apparently stable at relatively low levels of abundance up to the mid-1970s.

TABLE 2. Per mille age compositions of mature sand lance collected from the Grand Bank during the period 1968–79.

Age	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	Mean
1								14	14				2
2	6	63	4	116	4	45	44	105	376	179	159	82	105
3	115	196	87	333	139	187	203	172	297	368	452	437	254
4	427	273	271	255	457	340	400	161	141	171	261	303	279
5	324	231	381	235	275	280	202	186	79	94	45	111	200
6	91	154	196	46	84	106	92	155	55	73	30	40	94
7	30	63	50	9	35	34	48	81	21	55	18	17	39
8	3	21	4	5	6	6	6	52	10	31	13	6	14
9	3	—	—	—	—	—	6	36	4	15	13	5	7
10+	—	—	—	—	—	2	—	38	3	13	10	—	6
n	330	143	243	804	462	471	315	504	290	672	932	889	

TABLE 3. Age-specific lengths of mature sand lance from samples collected on the Grand Bank during the months April–July, 1969–79.

Year	Length-at-age (mm) 2	3	4	5	6	7	8	9	10+	$\sum_{2}^{6} G^b$
1969	166	200	214	226	240	247	243[a]			0.357
1970	165[a]	201	217	227	233	241	242[a]			0.202
1971	167	187	209	224	231	238	267[a]			0.386
1972	191[a]	194	208	225	237	246	253[a]			0.332
1973	191	201	219	228	239	253	260[a]	—	288[a]	0.200
1974	184	201	213	228	239	252	265	260	—	0.174
1975	170	192	212	224	234	238	250	250	263	0.291
1976	161	188	216	222	230[a]	246[a]	268[a]	—	—	0.386
1977	174	186	209	231	237	245	246	252	263[a]	0.265
1978	173	189	207	223	234	239	246	253	264[a]	0.343
1979	183	194	206	222	238	242	248[a]	—	—	
Mean	176	194	212	226	236	244	254	255	269	

[a]Less than or equal to five specimens.
[b]Relative growth coefficient.

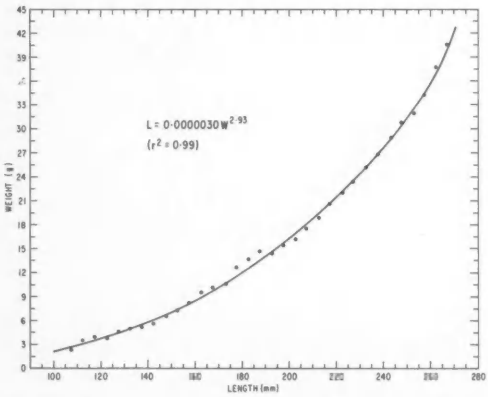

FIG. 5. Length–weight relationship of Grand Bank sand lance as determined from research samples collected during the second quarter of the year in the period 1968–79.

The 1968 year-class was relatively good and recruitment (measured at ages 2 and 3) of the most recent year-classes (1973 onwards) has been extremely strong (Table 4). On this basis sand lance abundance may be expected to remain high during the early 1980s.

ESTIMATION OF MORTALITY RATES

Several approaches were utilized to provide estimates of mortality rates. Initially a composite catch curve of mature sand lance was derived from the combined samples for the period 1968–79. This catch curve (Fig. 12A) is convex in shape, suggesting either increased mortality with age or temporal trends in recruitment and/or mortality. Survey data (Table 4) have shown that recruitment of sand lance has increased during the 1970s; in addition, examination of composite catch curves for the periods 1968–74 and 1975–79

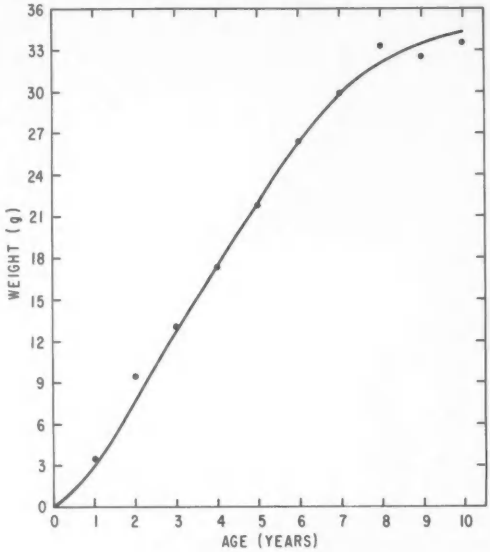

FIG. 6. Age–weight relationship of Grand Bank sand lance from research samples collected during the second quarter of the year.

indicates that mortality rates decreased substantially during the 1970s compared to the 1960s (Fig. 12B). Thus the convex curvature of the composite catch curve in Fig. 12A is probably the result of biasses due to temporal changes in both recruitment and mortality rates of sand lance during the time period under review.

Annual mortality rates as derived from analyses of catch curves for the year 1968–79 have been plotted against time (median year of the period covered by the catch curve) in Fig. 13. Considering all data points the slope is negative although the correlation coefficient is barely significant ($P = 0.03$). However, if one excludes median year 1966 (1969 sample year) because of its low sampling rate (Table 2), the residual points when plotted against time do produce a highly significant ($P \leq 0.01$) negative correlation. The regression equation thereby derived indicates that mortality rates of Grand Bank sand lance have decreased from levels of $Z \leq 1.0$ in the late 1960s to a level of $Z \geq 0.5$ in the mid- to late 1970s. This result is consistent with the evidence for decreasing mortality rates reflected in Fig. 12B. Because fishing mortality rates are negligible for Grand Bank sand lance (given the absence of a directed fishery), the above mortality estimates essentially represent the natural mortality rate. Although estimates of total mortality are available for the commercially exploited populations of sand lance in the North Sea (Reay 1970), precise estimates of natural mortality have not been made.

DETERMINANTS OF ANNUAL GROWTH

A relationship between growth during the 1st year of life and sea temperatures was earlier established for Grand Bank

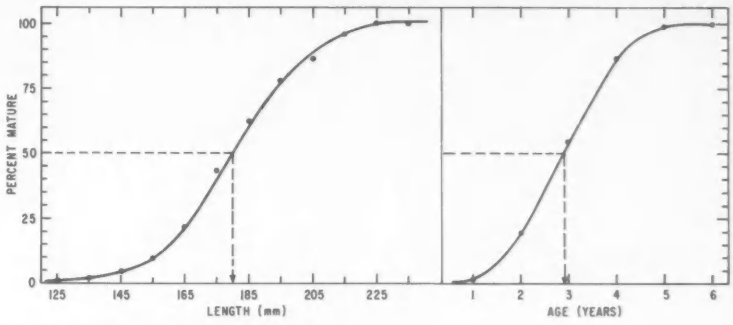

FIG. 7. Maturity ogives of Grand Bank sand lance.

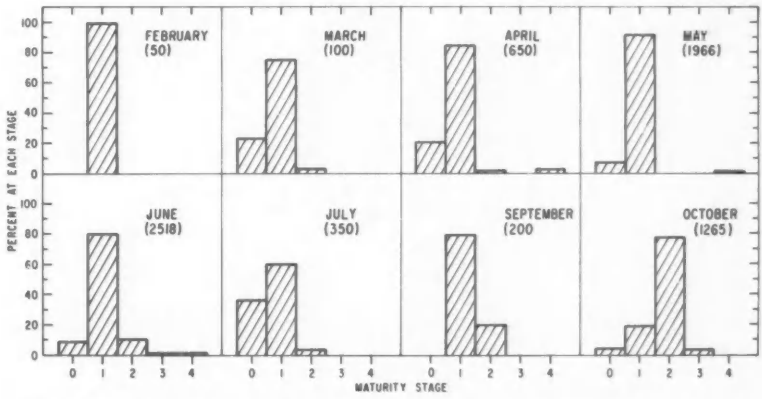

FIG. 8. Seasonal changes in maturation stages of Grand Bank sand lance (sample size in parenthesis).

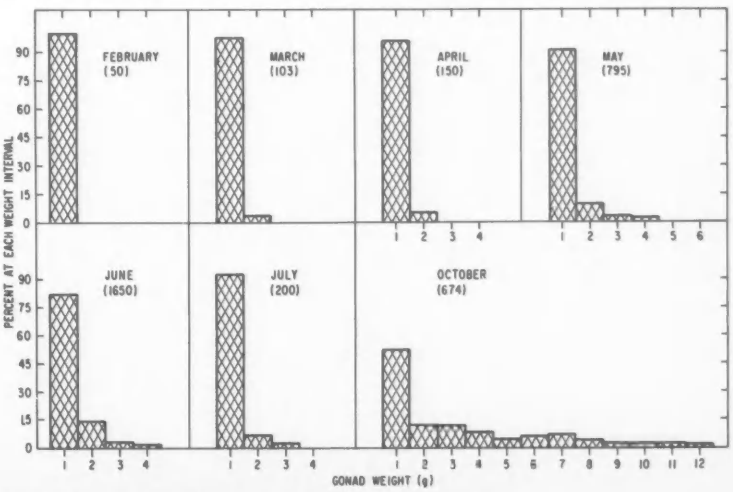

FIG. 9. Seasonal changes in gonad weight of Grand Bank sand lance.

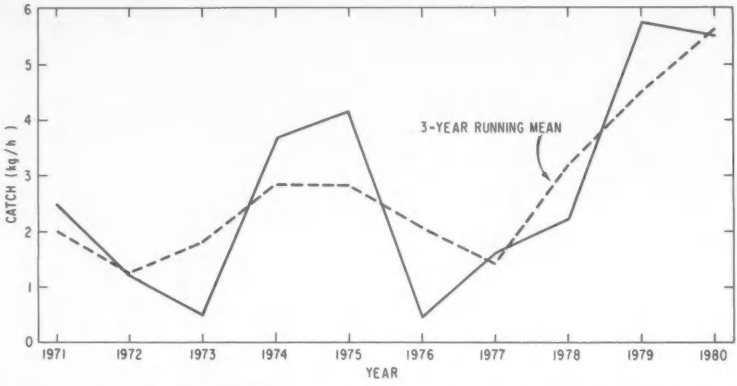

FIG. 10. Research Vessel CPUE (catch per unit effort) of sand lance in the random-stratified groundfish surveys on the Newfoundland Grand Bank in NAFO Div. 3LNO by the *A.T. Cameron* 1971–80.

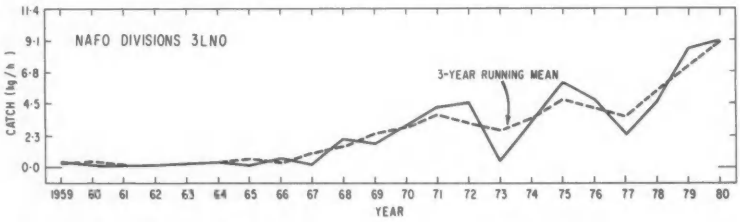

FIG. 11. Research Vessel CPUE of sand lance on the Newfoundland Grand Bank (NAFO Div. 3LNO) as derived from combined line transect groundfish surveys by the *A.T. Cameron* 1959–80.

TABLE 4. Age-specific catch rates of sand lance (immatures + matures) caught in research trawls of the *A.T. Cameron*, 1969–79.

	No. specimens per hour trawling										
Age	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
2	51	13	26	18	4	16	53	157	26	49	47
3	17	39	84	61	8	43	50	91	53	130	233
4	16	55	65	103	14	72	46	39	22	72	158
5	13	28	58	52	11	35	53	22	12	12	56
6	9	7	11	18	4	16	45	15	9	8	21
7	3.6	1	2.3	7.4	1.3	8	23	5.9	7	5	8.4
8	1.1	—	1.3	1.8	0.3	1.2	15	2.9	4	3.6	2.6
9	—	—	—	0.5	—	0.6	10	1.0	1.8	3.6	—
10+	—	—	—	—	0.1	—	11	1.0	1.7	2.7	1.1
Spec/h	110.7	143	250	261.7	42.7	191.8	307	334.8	136.5	285.9	527.1

sand lance (Winters 1981). Now I have examined adult growth, as expressed by the relative growth coefficient (Table 3) in relation to population density and an environmental signal, temperature. Hydrographic Station 27 located on the western side of the Avalon Channel (Fig. 1) has been selected as the environmental signal mainly because it is the only station with a long consistent time series and also because it is a good indicator of the flow of the Labrador current which greatly influences temperature patterns of the Grand Bank. A positive nonlinear relationship ($P \leq 0.01$) between sand lance growth and temperature is evident, (Fig. 14) particularly if one considers the 1970 point to be anomalous. This is not an unreasonable assumption as sampling intensity was poor for that year (Table 2). In addition independent observations from back-calculated (BC) data (with much greater sample sizes) provide the following estimates of the relative growth coefficient (RGC) for the years 1969–71 for which data are available:

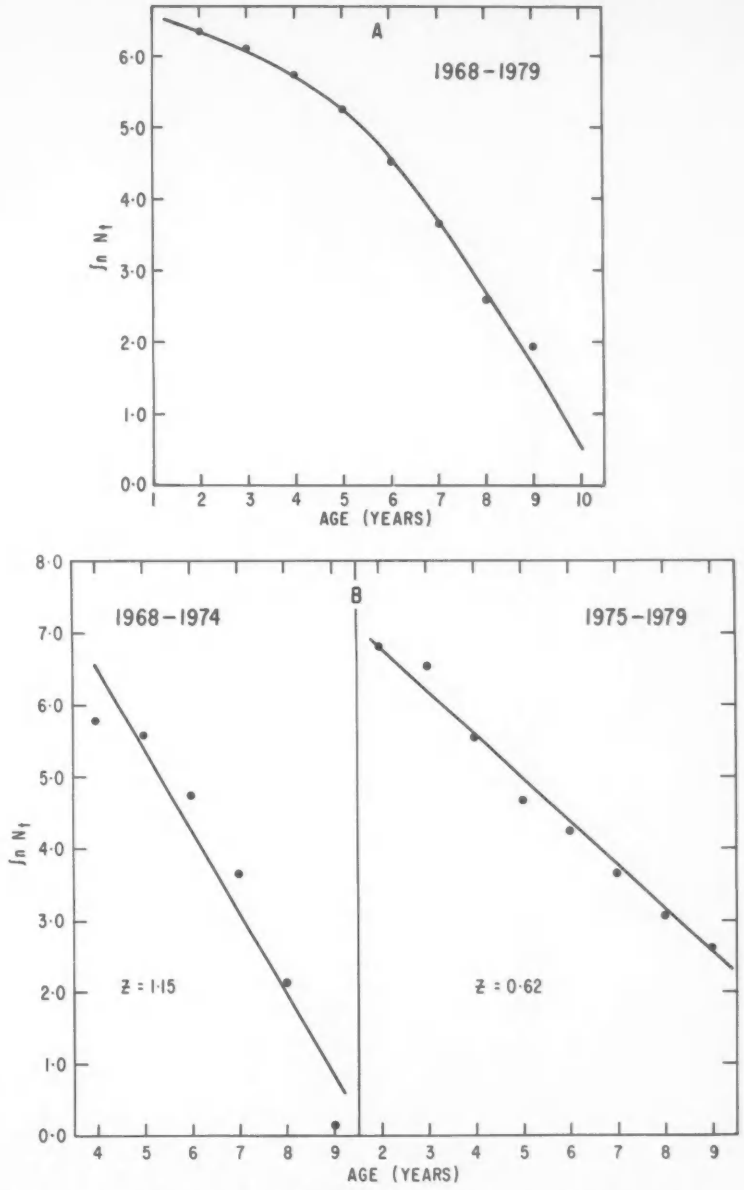

FIG. 12. Composite catch curves of mature sand lance from the Newfoundland Grand Bank.

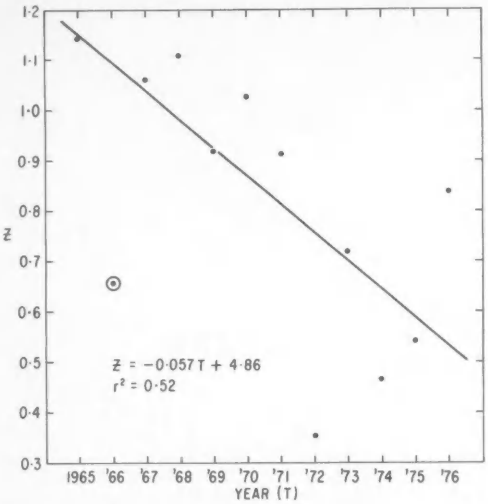

FIG. 13. Catch curve mortality estimates of Grand Bank sand lance plotted against the median year covered by each catch curve, i.e. median year = sampling year −3 yr.

	RGC	
Year	BC	Empirical
1969	0.328	0.357
1970	0.326	0.202
1971	0.401	0.386

Thus, accepting the anomaly of the 1970 point results in a highly significant nonlinear relationship between adult sand lance growth and temperature. When sand lance abundance (kg/h) is added, the coefficient of determination increases only slightly from $R^2 = 0.72$ to $R^2 = 0.74$.

Therefore I conclude that biomass is not a significant logistic factor of sand lance growth.

Discussion and Conclusion

Feeding studies have shown sand lance to be a major prey species in the marine food chain on the Newfoundland Grand Bank, particularly for cod and American plaice. These two species have undergone major fishery-induced changes in

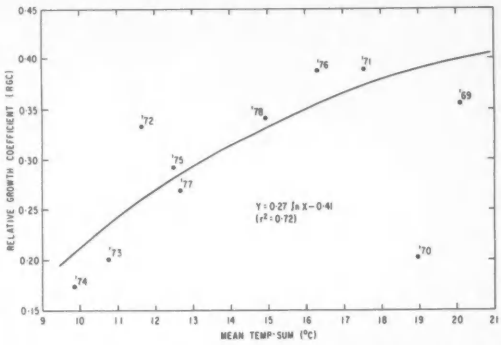

FIG. 14. Relationship between the relative growth coefficient of Grand Bank sand lance and Station 27 January−November summed temperatures (mean for the 0- to 100-m depth).

abundance since the mid-1960s; the cod stock has been reduced from a level of nearly 500 000 t in the late 1960s to less than 100 000 t in 1980 (Bishop and Gavaris 1981), whereas American plaice declined from a biomass of 400 000 t to less than 200 000 t in 1973 but has recovered to original levels since then (Pitt and Brodie 1980). In addition, capelin, the other important prey species on the Grand Bank, has also fluctuated in abundance during this period (Carscadden et al. 1981). To investigate these potentially interacting factors I carried out simple correlation analyses between sand lance abundance (research vessel index) and recruitment (measured at ages 2 and 3) and cod biomass (midyear 2+), American plaice biomass (midyear 6+), capelin biomass (3+), and recruitment (at age 2) (Table 5). A highly significant negative correlation resulted between sand lance abundance and cod biomass, and a significant negative correlation was obtained between sand lance recruitment and cod biomass. The negative correlation between cod biomass and sand lance abundance is consistent with the apparent decline in the mortality rate of sand lance since the late 1960s. The positive (but nonsignificant) relationship between American plaice biomass and both sand lance abundance and recruitment is surprising as feeding studies have shown sand lance to be the most important prey species in the diet of American plaice on the Grand Bank (Pitt 1973). This statistical relationship is probably spurious given the negative correlation between cod biomass and American plaice biomass and the much greater consumptive capacity of cod in relation to American plaice. Preliminary studies (G. Lilly, Northwest Atlantic

TABLE 5. Correlation matrix of various variables considered in relation to sand lance abundance on Grand Bank. (*$P \leq 0.01$.)

	SLA	SLR	CAB	CAR	COB	APB
Sand lance abundance (SLA)	1.00	0.44	−0.27	−0.08	−0.80*	0.49
Sand lance recruitment (SLR)		1.00	0.51	−0.01	−0.73	0.28
Capelin biomass (CAB)			1.00	−0.38	−0.31	0.11
Capelin recruitment (CAR)				1.00	−0.04	−0.49
Cod biomass (COB)					1.00	−0.30
American plaice biomass (APB)						1.00

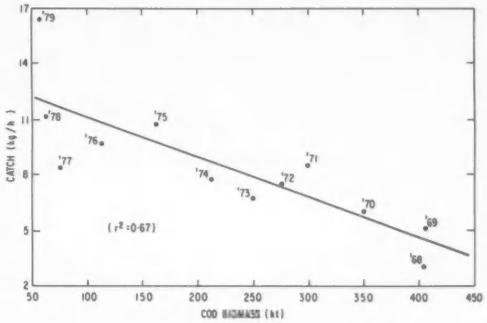

FIG. 15. Relationship between Research Vessel CPUE abundance indices of Grand Bank sand lance and cod biomass (mean of the 3 yr previous).

Fisheries Centre, St. John's, Nfld., Canada, personal communication) have shown that cod of an average commercial size (50–55 cm) have a stomach capacity 7.5 times greater than that of an average size (40–55 cm) American plaice. Accepting that the total weight ratio of cod to American plaice in these size ranges is about 2.2 (1.0 kg vs. 0.45 kg) implies that per unit biomass the consumptive capacity of cod is about 3.5 times that of American plaice, assuming the same digestion rates. Thus cod would have been expected to contribute much more to the variability of sand lance abundance on the Grand Bank than American plaice. Figure 15 illustrates this relationship for the period 1968–79. Because the present management strategy of the Northwest Atlantic Fisheries Organization (NAFO) for the Grand Bank cod stock is a rapid rebuilding to take advantage of a recent strong year-class, an increase in the natural mortality rate of sand lance and a commensurate decline in its abundance may be expected during the early 1980s.

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Normal Ranges for Diagnostically Important Hematological and Blood Chemistry Characteristics of Rainbow Trout (*Salmo gairdneri*)

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MILLER, W. R. III, A. C. HENDRICKS, AND J. CAIRNS JR. 1983. Normal ranges for diagnostically important hematological and blood chemistry characteristics of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 40: 420–425.

Wytheville strain rainbow trout (*Salmo gairdneri*) were used in an 11-mo study designed to establish normal ranges for several hematological and blood chemistry characteristics. Two nonparametric techniques, percentile estimation and tolerance interval, were used and produced comparable ranges to those based on the Gaussian distribution. Serum glucose levels appeared to coincide with the condition of the gonads; low glucose levels corresponded with approximate spawning times at the hatchery. Total serum protein and gonadal condition were similarly related. High variability of the serum enzymes LDH and SGOT was partially explained by a positive linear relationship between enzyme activity and acclimation temperatures. In addition to physiological significance, determination of normal ranges for rainbow trout has promise in diagnosis of pathological, disease, and toxicant-induced stresses.

MILLER, W. R. III, A. C. HENDRICKS, AND J. CAIRNS JR. 1983. Normal ranges for diagnostically important hematological and blood chemistry characteristics of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 40: 420–425.

Des truites arc-en-ciel (*Salmo gairdneri*) de la lignée de Wytheville ont été utilisées dans une étude de 11 mois conçue dans le but de déterminer les gammes normales de plusieurs caractéristiques hématologiques et de la chimie du sang. Deux méthodes non paramétriques ont été utilisées, l'estimation percentile et l'intervalle de tolérance. Les deux ont donné des résultats comparables à ceux fondés sur une distribution de Gauss. Les niveaux de glucose sérique semblent coïncider avec l'état des gonades, de bas niveaux correspondant au moment approximatif de la ponte à l'écloserie. Il y a également corrélation entre les protéines sériques totales et l'état des gonades. La forte variabilité des enzymes sériques LDH et SGOT s'explique partiellement par une relation linéaire entre l'activité enzymatique et les températures d'acclimatation. En plus de sa signification physiologique, la détermination des gammes normales chez la truite arc-en-ciel offre des possibilités diagnostiques dans les cas de stress pathologique ou déclenché par des substances toxiques.

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AN area that requires further research in fish hematology and blood chemistry is the method used to determine normal ranges for diagnostic characteristics. Reed et al. (1971) suggested two nonparametric techniques for determining normal ranges. These techniques were the percentile estimation and tolerance interval approaches. By comparing these nonparametric techniques with Gaussian or log-Gaussian estimates, nonparametric estimates were demonstrated to be as accurate as Gaussian or log-Gaussian estimates if the normal distribution assumptions happen to be true. If Gaussian assumptions are inappropriate, corresponding estimates can be biased, whereas nonparametric techniques apply regardless of distribution.

The purpose of this study was to compare normal range estimates for several hematological and blood chemistry characteristics of rainbow trout (*Salmo gairdneri*) using nonparametric and Gaussian techniques. Additionally, effects of

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TABLE 1. General statistics for hematological and blood chemistry characteristics of rainbow trout (*Salmo gairdneri*) — Wytheville strain.

Characteristic	*n*	Mean	SD	CV	Median	Prob:*D*	99%	1%	Range
Total protein ($g \cdot dL^{-1}$)	122	2.25	0.5	22.4	2.1	0.01	3.8	1.5	2.4
Albumin ($g \cdot dL^{-1}$)	122	1.65	0.4	23.6	1.6	0.01	2.9	1.0	1.9
P_i ($mg \cdot dL^{-1}$)[a]	122	8.68	1.5	17.6	8.65	0.15	12.4	5.0	7.4
Mg ($mmoL \cdot L^{-1}$)	122	4.82	0.8	34.8	5.0	0.01	8.4	2.2	6.2
Alk. Phos. (IU)[b]	122	50	23.0	46.3	46.8	0.01	114.5	18	98.7
LDH (IU)	122	979	360.0	40.4	923	0.01	2313	406	1911.9
SGOT (IU)[a]	122	680	313.0	45.9	645	0.07	1920	207	1736.1
Glucose ($mg \cdot dL^{-1}$)	122	144	40.7	28.3	154	0.01	253	63	195.3
Albumin ($g \cdot dL^{-1}$) / Total protein ($g \cdot dL^{-1}$)	122	0.73	0.08	11.2	0.72	0.01	0.9	0.5	0.4
Hematocrit (%)[a]	122	32.0	5.5	17.1	31.5	0.15	49.0	21.0	29.5
Red blood cell count[a] ($millions \cdot mm^{-3}$)	122	1.18	0.2	19.7	1.15	0.15	1.9	0.44	1.6
Hemoglobin ($g \cdot dL^{-1}$)	122	5.0	1.6	31.8	5.24	0.04	8.3	1.3	7.3
MCHC (%)[a]	122	15.6	4.8	30.8	15.7	0.15	24.5	3.9	20.7
MCH (pg)	122	43.1	13.5	31.4	44.9	0.01	76.5	8.2	70.3
MCV (μm^3)	122	280.8	75.2	26.8	280	0.01	779.2	182.0	693.7

[a]Parameters for which there is insufficient reason to doubt normality as determined by the Kolmogorov–Smirnov *D*-test ($\alpha \geq 0.05$).

[b]International units per litre — amount of enzyme catalyzing the transformation of 1 μmol of substrate per minute.

sexual maturity and acclimation temperatures were examined to determine their impact on the normal range of several blood chemistry characteristics.

Materials and Methods

Blood Collection and Analysis

Two-year-old rainbow trout (average weight (SD) 239 (61) g) were obtained from the Wytheville National Fish Hatchery, Grahams Forge, Virginia. Upon arrival at the laboratory, two groups of 10 animals each were placed in 662-L (175-gal) aquaria equipped with Frigid Unit chillers. Dechlorinated tapwater was supplied to the aquaria at the rate of $9\ L \cdot min^{-1}$ during the cooler months and $1\ L \cdot min^{-1}$ during the summer. Over the 11-mo experimental period, the following water chemistry data were recorded: temperature, 3–25°C; dissolved oxygen, 7.2–11.1 $mg \cdot L^{-1}$; alkalinity, 18.3–46.7 $mg \cdot L^{-1}$ as $CaCO_3$; hardness, 39.3–61.1 $mg \cdot L^{-1}$ as $CaCO_3$; and pH, 6.5–7.4.

Fish were stunned by a blow to the head, the heart was exposed, and blood samples taken by cardiac puncture from the bulbous arteriosus using a syringe rinsed with ammonium heparin. Whole blood was placed in chilled 15-mL centrifuge tubes and allowed to clot for 3 h. Serum was separated after centrifugation at 1000 *g* for 15 min at 4°C, and stored for future analyses at −15°C.

A 20-μL aliquot of whole blood was removed for hemoglobin determination using the technique described by Blaxhall and Daisley (1973). Blood for hematocrits and red blood cell (RBC) counts was obtained by severing the caudal peduncle. Hematocrits were determined using the method of Wintrobe (1974). The RBC counts were made using techniques suggested by Hesser (1960). Hendricks' (1952) solution was used as the diluent for RBC counts. The RBC count was reported as the mean of three fields of 80 squares. The RBC indices mean corpuscular hemoglobin concentration (MCHC), mean corpuscular hemoglobin (MCH), and mean corpuscular volume (MCV) were calculated using formulae presented by Wintrobe (1974). After blood collection, the gonads were weighed. Over an 11-mo period, 122 rainbow trout were examined in this fashion.

Serum was analyzed within 48 h of collection on a Gilford 3500 computer directed analyzer. Factors measured included albumin, alkaline phosphatase (EC 3.1.3.1), glutamic-oxaloacetic transaminase (EC 2.6.1.1), glucose, inorganic phosphorous, lactate dehydrogenase (EC 1.1.1.27), magnesium, and total protein. During each analysis, appropriate standards and/or human control sera were used.

Nonparametric and Parametric Techniques

Data were analyzed by calculating: number of observations (*n*), means, standard deviations (SD), coefficients of variation (CV), medians, Kolmogorov–Smirnov probability statement (Prob:*D*), 99 and 1 percentiles, the range of observations, and the skewness and kurtosis. The Kolmogorov–Smirnov *D*-statistic with the associated Prob:*D* provided a means of testing the null hypothesis that data values were a random sample from a normal distribution. The null hypothesis was rejected for large values of *D* that had an associated probability of $P < 0.05$.

Normal ranges were established for each characteristic using two nonparametric techniques; the percentile estimation (PE) of Reed et al. (1971) and the tolerance interval method (Brunden et al. 1970). Parametric limits were calculated using the suggested techniques of Hoffman (1963). Frequency distributions were developed for each blood chemistry and hematological characteristic.

Results

Data for 15 hematological and blood chemistry characteristics are presented in Table 1. Data variability (indexed by

TABLE 2. A summary of normal range estimates for rainbow trout, *Salmo gairdneri* — Wytheville strain.

Characteristic	Percentile estimation		Percentile estimation		95–50 tolerance interval	Gaussian range
	Lower limit	Upper limit	90% CI lower	90% CI upper		
Total protein ($g \cdot dL^{-1}$)	1.6	3.5	1.5–2.1	3.3–3.9	1.6–3.5	1.2–3.3
Albumin ($g \cdot dL^{-1}$)	1.1	2.7	1.0–1.47	2.4–2.9	1.1–2.7	0.9–2.4
Mg ($mmoL \cdot L^{-1}$)	2.2	8.2	2.2–3.4	7.0–8.4	2.4–8.2	1.4–8.2
P_I ($mg \cdot dL^{-1}$)[a]	5.1	12.0	5.0–6.3	11.4–12.0	5.1–12.0	5.7–11.7
Alk. Phos. (IU)[b]	19	91	18–20	84–117	18.3–90.9	3.7–95.9
LDH (IU)	412	1906	406–486	1727–2318	407–1907	188–1770
SGOT (IU)[a]	217	1520	206–254	1113–1942	212–1539	55–1305
Glucose ($mg \cdot dL^{-1}$)	72	218	61–77	191–256	71–218	62–225
Albumin ($g \cdot dL^{-1}$) / Total protein ($g \cdot dL^{-1}$)	0.54	0.92	0.51–0.62	0.86–0.93	0.53–0.92	0.57–0.90
HCT (%)[a]	21.5	43.9	21.0–25.5	41.0–50.5	21.5–44.0	21.1–43.0
Blood cell count ($millions \cdot mm^{-3}$)	0.77	1.67	0.36–0.86	1.55–1.96	0.70–1.68	0.72–1.64
Hb ($g \cdot dL^{-1}$)	1.5	7.7	1.2–2.2	7.4–8.5	1.5–7.7	1.8–8.1
MCHC (%)[a]	5.6	24.4	3.8–6.6	23.4–24.5	4.0–24.4	6.0–25.3
MCH (pg)	14.4	70.0	7.9–18.0	61.3–78.2	9.2–70.1	16.1–70.2
MCV (μm^3)	192	420	181–198	372–875	184–421	130–431

[a]Parameters for which there was insufficient reason to doubt normality as determined by the Kolmogorov–Smirnov *D*-test ($\alpha \geq 0.05$).

[b]International units per litre — amount of enzyme catalyzing the transformation of 1 μmol of substrate per minute.

CV) was highest for Mg, alkaline phosphatase, LDH, and SGOT. Using the Kolmogorov–Smirnov Prob:*D*, 5 of 15 characteristics, these being inorganic phosphorous (P_I), SGOT, hematocrit, RBC count, and MCHC, were shown to have insufficient reason to doubt normality. Further, nonparametric statistics appeared appropriate for compiling normal ranges for the 15 blood chemistry and hematological characteristics (see Table 2).

The PE, with 90% confidence intervals about the upper and lower limits, the 95–50 TI, and, for comparison, the traditional Gaussian ranges (i.e. mean ± 2 SD) are given. Close agreement, as might be expected, occurred between limits calculated using the two nonparametric techniques. However, comparatively good agreement also occurred between the two nonparametric techniques and the Gaussian ranges. To examine these relationships, frequency distributions were developed for the 15 characteristics (Fig. 1).

A positive value for skewness (*S*) indicated skewness to the right, whereas a negative *S* indicated skewness to the left. Platykurtosis was indexed by a negative kurtosis (*K*) value, and leptokurtosis was indexed by a positive *K* value. There was insufficient evidence to doubt that P_I, SGOT, hematocrit, RBC, and MCHC were normally distributed. Of these five distributions, the distribution for SGOT had the lowest Kolmogorov–Smirnov probability of $P = 0.07$ which was reflected in the comparatively high values for *S* and *K*. Sufficient evidence to doubt normality occurred in 70% of the remaining 10 distributions which were skewed to the right and typically leptokurtic.

Serum-glucose levels fluctuated with gonad weights of both males and females (Fig. 2) with the lowest points corresponding to peak gonadal development. Peaks in gonad weights correlated with approximate spawning times at the hatchery. A similar pattern was observed for total serum protein and gonad weights (Fig. 3).

Acclimation temperature appeared to contribute to the high coefficients of variation for the serum enzymes LDH and SGOT (Fig. 4, 5). Both LDH and SGOT showed a positive linear relationship with acclimation temperatures; no significant linear relationship was noted for alkaline phosphatase activity and acclimation temperature.

Discussion

Parametric and Nonparametric Techniques for Establishing Normal Ranges

From our data from 122 animals over an 11-mo period, we conclude that two-thirds of the 15 hematological and physical characteristics are not normally distributed. Reed et al. (1971) suggested that if the underlying distribution was not known, then a nonparametric technique would be less subject to error than a parametric one. The decision to use nonparametric statistics (percentile estimation and tolerance interval) in setting normal ranges for rainbow trout blood chemistry characteristics was therefore justified.

Wedemeyer and Nelson (1975) compared the PE, TI, and Gaussian methods for approximating normal ranges for 10 blood chemistry parameters of the Shasta strain of rainbow trout. Data were compiled for 200 juveniles in the 40- to 80-g size-class. The percentile estimate produced the more acceptable normal range estimates. McCarthy et al. (1973) presented results for 14-mo-old Kamloops strain rainbow trout. In addition to calculating basic statistics on 50 animals, a 96 percentile range was provided. A comparison of the results for the two previous studies and the present work on Wytheville strain rainbow trout is presented in Table 3. Most estimates, with the exception of hemoglobin and total protein,

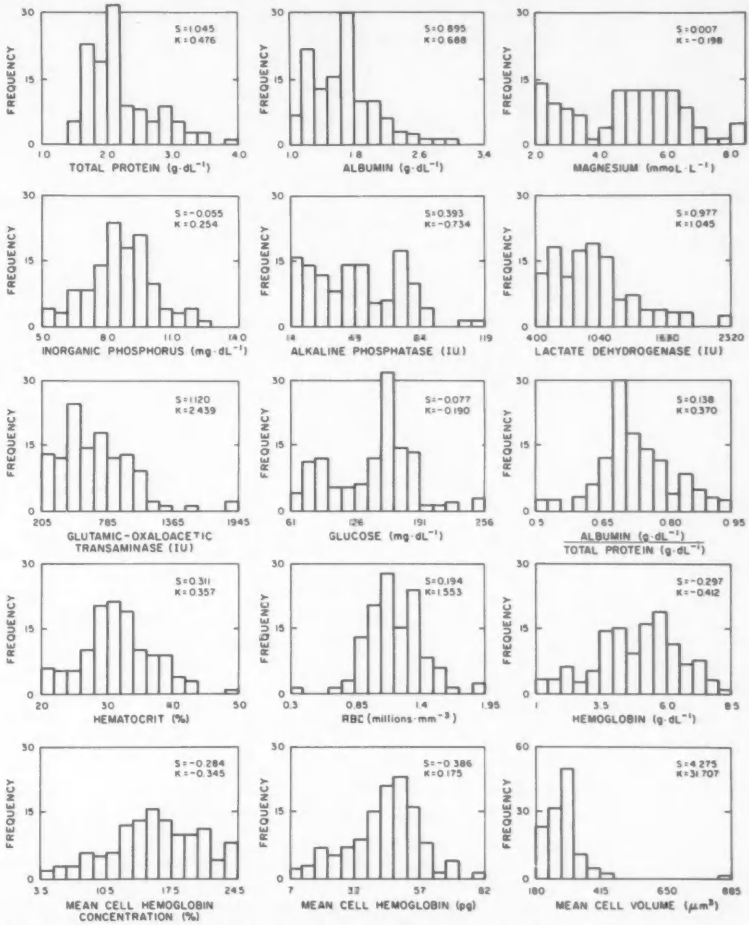

FIG. 1. Frequency distributions for blood chemistry characteristics of rainbow trout showing the skewed (S) and kurtic (K) nature of these data. Most of these characteristics were not normally distributed.

agreed favorably. Differences in hemoglobin perhaps reflect the wide temperature variations (3−25°C) during this study as compared to constant temperatures for the Wedemeyer and Nelson study (1975) and the McCarthy et al. study (1973). Acclimation temperatures affect hemoglobin levels as well as RBC indices (DeWilde and Houston 1967). Differences in total protein were likely due to the use of plasma by McCarthy et al. (1973).

Comparison of the two nonparametric techniques (i.e. PE and TI) showed that comparable results could be obtained by both. An advantage of PE was that confidence intervals could be described about the upper and lower limits. However, values for the PE limits were interpolated and do not reflect actual observations. The TI method had the advantage of using actual data points to define normal ranges.

The frequency distributions in Fig. 1 illustrate an important point in determining the statistics to use in establishing normal ranges. In only a few cases do the mean and standard deviation completely describe the distribution — a characteristic of normal distributions as stated in the central-limit theorem (Siegel 1956).

Nonparametric techniques, however, do have a disadvantage in that extreme values, in small data sets, tend to define normal ranges. If all observations are from healthy individuals, extreme values are of less importance. However, if abnormal, diseased individuals are included, this may significantly affect the normal ranges.

Sexual Maturity and Acclimation Temperature

Glucose and total protein reached their lowest values at points corresponding to the highest gonad weights (Fig. 2, 3).

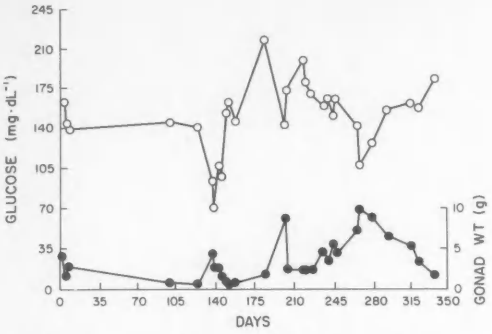

FIG. 2. The influence of gonad weights (●) on serum glucose concentrations (○) over an 11-mo period. Each circle represents the mean of at least four (♂ and ♀ pooled) individuals.

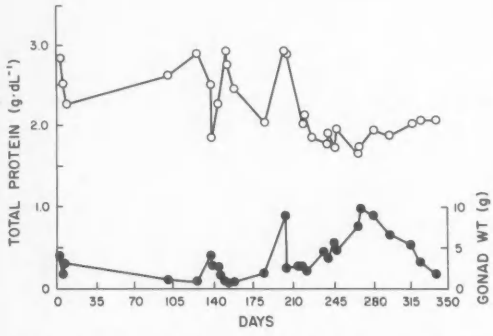

FIG. 3. The influence of gonad weights (●) on total serum protein concentrations (○) over an 11-mo period. Each circle represents the mean of at least four (♂ and ♀ pooled) individuals.

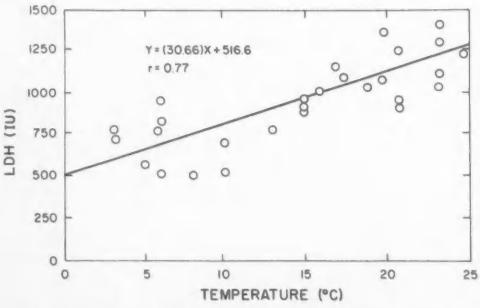

FIG. 4. Regression line showing how acclimation temperatures might contribute to high variability in lactate dehydrogenase (LDH) activity. Each circle represents the mean of at least four (♂ and ♀ pooled) individuals.

MacLeod et al. (1960) observed that total serum protein of coho salmon (*Oncorhynchus kisutch*) was lowest in animals with the highest gonad-to-body weight ratio.

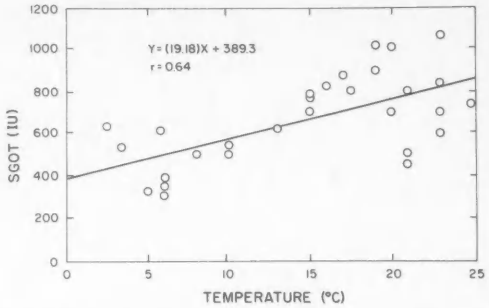

FIG. 5. Regression line showing how acclimation temperatures might contribute to high variability in serum glutamic-oxaloacetic transaminase (SGOT) activity. Each circle represents the mean of at least four (♂ and ♀ pooled) individuals.

TABLE 3. A comparison of normal ranges from this study on Wytheville strain rainbow trout to results of work on Shasta[a] and Kamloops[b] strains.

Characteristic	Shasta	Kamloops	Wytheville
Hematocrit (%)	24.0–43.0	32–48	21.5–43.9
Hemoglobin ($g \cdot dL^{-1}$)	5.4–9.3	5.6–10.3	1.5–7.7
RBC (millions $\cdot mm^{-3}$)	NR[c]	0.77–1.58	0.77–1.67
MCHC (%)	NR	12.7–25.3	5.6–24.4
MCH (pg)	NR	54–98	14–70
MCV (μm^3)	NR	274–513	192–420
Mg ($mmoL \cdot L^{-1}$)	2.4–6.6	NR	2.2–8.2
P_i ($mg \cdot dL^{-1}$)	8.4–12.7	NR	5.1–12.0
Total protein ($g \cdot dL^{-1}$)	NR	4.0–6.6	1.6–3.49
Glucose ($mg \cdot dL^{-1}$)	NR	71–207	72–218

[a]After Wedemeyer and Nelson (1975).
[b]After McCarthy et al. (1973).
[c]Not reported.

Jonas and MacLeod (1960) reported that glucose and total protein decreased during the spawning migrations of sockeye salmon (*Oncorhynchus nerka*). The significant drop in total protein was more than might be accounted for by blood dilution.

Robertson et al. (1961) postulated that salmon become hyperglycemic during sexual maturation (spawning run) as a result of gluconeogenesis from the action of adrenal corticoids on muscle and fat deposits. Similar observations by Lysaya (1951) prompted him to conclude that the blood sugar of salmon was very high and that individual fluctuations are conditioned by the state of the gonads. Chavin and Young (1970) observed that goldfish (*Carassius auratus*) serum glucose was unaffected by starvation periods of up to 151 d. A similar observation was noted by Sakamoto and Yone (1978) using Red Sea bream (*Chrysophrys major*).

It may be hypothesized that as a trout, male or female, builds up a gonadal mass (eggs or milt), the constituents of the gonads (e.g. carbohydrates and proteins) must be mobilized from existing stores of these constituents and/or catabolized from other constituents. The presence of high concentrations

of glucocorticoids (e.g. cortisone) could be responsible for the increase in serum-glucose levels prior to spawning. At spawning, body stores of protein and glycogen are depleted, thus resulting in reduced levels of serum glucose and total protein.

Another factor which could partially explain the variability of rainbow trout blood chemistry parameters is water temperature. Effects of acclimation temperatures were particularly acute with regard to enzyme activities (Fig. 4 and 5). As acclimation temperatures increased, enzymatic activities for LDH and SGOT increased in a linear fashion. A similar observation was made by Sauer and Haider (1977) on effects of water temperature on serum LDH and SGOT of rainbow trout. It was observed that LDH activity was 10 times higher at 21.5 vs. 3.5°C. Activities for SGOT were twice as high at 19.0 vs. 3.5°C. Alkaline phosphatase activity was not related to acclimation temperature; an observation corroborated in this investigation. An in vitro study by Warner et al. (1978) showed that LDH, SGOT, and alkaline phosphatase activities increased linearly with assay temperatures.

Observations during this study indicated that comparable normal ranges can be obtained for fish blood chemistry characteristics using either nonparametric or Gaussian techniques. Nonparametric techniques, however, are to be preferred because a priori assumptions regarding a Gaussian distribution may not apply to many blood values of rainbow trout. It was also demonstrated that serum glucose and total protein are affected by gonadal condition. Acclimation temperatures were also shown to influence serum enzyme activity. Consequently, determination of normal ranges must be viewed in a context that considers distributional characteristics, sexual influences, sexual maturation, and acclimation temperature.

A logical goal of fish hematological studies is the diagnosis of disease, pathological and toxicant-induced stresses. However, before reaching this goal, studies must continue on the determination of the normal condition.

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Early Marine Mortality of Marked Juvenile Chum Salmon (*Oncorhynchus keta*) Released into Hood Canal, Puget Sound, Washington, in 1980[1]

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BAX, N. J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Can. J. Fish. Aquat. Sci. 40: 426–435.

The average daily loss in numbers from a group of fluorescently marked, hatchery-reared, juvenile chum salmon (*Oncorhynchus keta*) remaining in the nearshore zone following their release from the hatchery into southern Hood Canal, Washington State, was estimated at 38–49%. This estimated loss was then adjusted by the estimated maximum emigration of marked fish from the sampling area and the average daily mortality over a 2- and a 4-d time period estimated at between 31 and 46%. These estimates are an order of magnitude higher than estimates of the average daily mortality of naturally emigrating juvenile pink salmon (*O. gorbuscha*) from the Bella Coola River, British Columbia, over a 40-d time period (Parker 1968). The two studies are contrasted and it is suggested that daily mortality is highly variable over the 40 d subsequent to saltwater entry, with mortality higher initially, particularly for those fish remaining close to their point of saltwater entry.

BAX, N. J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Can. J. Fish. Aquat. Sci. 40: 426–435.

On estime à 38–49 % la proportion perdue quotidiennement de sujets d'un groupe de saumoneaux keta (*Oncorhynchus keta*) de pisciculture marqués par fluorescence et séjournant à proximité de la côte après leur mise en liberté dans la partie méridionale du canal Hood, dans l'État de Washington. Ces pertes estimées sont ensuite ajustées d'après le maximum estimé d'émigration, hors de la zone d'échantillonnage, de poissons marqués et la mortalité quotidienne, durant des périodes de 2 et 4 d, estimée à 31 et 46 %. Ces estimations dépassent d'un facteur celles de la mortalité quotidienne de jeunes saumons roses (*O. gorbuscha*) émigrant naturellement hors de la rivière Bella Coola, en Colombie-Britannique, durant une période de 40 d (Parker 1968). Une comparaison des deux études nous porte à croire que la mortalité quotidienne est très variable durant les 40 jours qui suivent l'entrée en eau salée. Elle est plus prononcée au début, surtout chez les poissons qui ne s'éloignent pas de leur point d'entrée en eau salée.

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IT was the purpose of this study to execute a short-term mark and recapture program to estimate the mortality of juvenile chum salmon (*Oncorhynchus keta*) over the first 2- and 4-d intervals immediately following their release from a hatchery. This project continued studies initiated by the Fisheries Research Institute of the University of Washington in 1975, on the salmon outmigrations in Hood Canal.

Early marine residence is regarded by many as being a critical phase in the life history of chum salmon significantly affecting the numerical strength of the adult return (Bakkala 1970; Peterman 1978; Sakuramoto and Yamada 1980). For example, Gilhousen (1962) studying pink salmon (*O. gorbuscha*) from the Fraser River stated that "conditions in the marine environment have been so variable that variation in fry abundance has had a secondary effect on total survival." With the exception of Parker's estimates of 2–4% average daily mortality for pink salmon from the Bella Coola River during the first 40 d of marine life (Parker 1968), there are few estimates available for salmonid mortality during their initial period in the marine environment. Even within this 40-d period average rates may be misleading (Parker 1968). Burrows (1969) found evidence of a high estuarine mortality and large changes in physiological characteristics in the 7 d between the release and recapture of chinook salmon (*O. tshawytscha*) smolts. Preliminary estimates based on recaptures of juvenile chum salmon released from the Big Beef Creek hatchery into Hood Canal suggested that the mortality over the first 2 d was 29 and 44% in February of 1978 and 1979, respectively (Bax unpublished data). This paper presents the results of a mark and recapture study on juvenile chum salmon released from a hatchery at Enetai in southern Hood Canal in May of 1980.

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Materials and Methods

Study Area

Hood Canal is a branch of the Puget Sound system in the northwest corner of Washington State (Fig. 1). It is oriented approximately NNE to SSW (30°) and is ~95-km long with widths varying from 2 to 5 km, except in the middle reaches at Dabob Bay. An entrance sill 60 m in depth, ~20 km from the mouth, separates it from the main basin of Puget Sound. The maximum depth of Hood Canal is 185 m. Hood Canal is an example of a positive fjord-type estuary with a net outflow at the surface and a net inflow at depth (Winter et al. 1975).

Artificial propagation programs and natural production contribute to the juvenile salmon emigrating through Hood Canal. Previous mark and recapture studies on juvenile chum salmon released from hatcheries into Hood Canal have indicated an initial dispersal of the juveniles to areas north and south of the release point on both shores, followed by a northerly movement out of the Canal. The mean rate of northerly movement ranged from 14 km/d in February to 4 km/d in May and June (C. J. Whitmus, School of Fisheries, University of Washington, Seattle, WA 98195, unpublished data).

Sampling in this study was designed to assess the daily distribution of marked fish released from the Point No Point Treaty Council's hatchery at Enetai in southern Hood Canal. The sampling area extended from 10 km southeast of Enetai to 25 km north of Enetai, on the east and west shores. The choice of sampling sites within this area was restricted by the requirement of moderately sloping beaches with few obstructions to facilitate efficient retrieval of the beach seine. Sampling sites were, on average, 3 km apart. Townet transect locations were directly offshore from the beach seine sites.

There was insufficient time to sample all sites daily. Priority was given to sampling directed at defining the peak abundance of the released groups. Sampling for the extent of their distributions was done as time permitted, and resulted in the east shore sampling being incomplete, especially at the northern end of the distributions. For this reason data from the east shore were not used in the estimates of mortality. These data will be used to compare the proportion of each marked group crossing to the east shore upon release. There were few recaptures of marked fish with the townet, and the changing distribution of those few recaptures indicated that there was emigration from the area surveyed by the townet. There were sufficient recaptures of marked fish by the beach seine on the west shore to indicate a stable distribution of the marked fish in this area. Accordingly, only the data set for the west shore area sampled by the beach seine was used to estimate mortality, and only this area is referred to as the "sampling area" subsequently in this paper.

Origin and Treatment of Fish

The chum salmon used in this study were reared in spring water at Enetai from eggs collected at the Quilcene National Fish Hatchery, 55 km north of Enetai (Fig. 1). Previous releases at Enetai of 1.9, 1.8, and 2.2 million juveniles reared from eggs of the same source in 1977, 1978, and 1979 have resulted in returns of 3224 and 5096 adults to Enetai in 1980 and 1981 (chum salmon in Hood Canal return principally as 3- and 4-yr-old fish). This indicates a higher rate of return than that to the Quilcene National Fish Hatchery where returns of 2071 and 1672 adults resulted from releases of 6.1, 4.7, and 4.2 million juveniles over the same time periods. No data are available for the contribution from the fish released at Enetai to the fishery.

The fish were reared in 7.32-m-diameter pools with a water depth of ~1 m. The final rearing density was estimated at 300 000 fish per pool. The fish were fed until 2 d before they were marked. They were not fed in the 3- to 5-d period between marking and their release or their transfer into saltwater pens.

The first marked group was released directly from the hatchery in the evening of May 18, by removing the central standpipe in the rearing pools so that the fish were washed down a 20-cm-diameter pipe to the ½-km creek leading to Hood Canal. In the same evening the second and third marked groups were transported by road in an oxygenated planting tank to separate 1.2-m cubic net pens of 3.2-mm mesh, moored in an unused section of a marina at Hoodsport, 6 km north of the hatchery. The fish were not fed while in these pens. These two groups were released in the evenings of May 20 and May 22. Each group was transported to the release site in two planting tanks aboard the R/V *Tenas*. The planting tanks were supplied with circulating salt water and oxygen. Dissolved oxygen concentrations were monitored continuously and remained above 7 ppt at all times.

Fluorescent Pigment Marking Techniques

The marking of juvenile fish with fluorescent pigment, as described by Jackson (1959), is an efficient and economical technique for marking large numbers of juvenile chum salmon. Fluorescent pigment particles (70% between 30 and 350 μm) were forced through the epidermis and into the dermis of the juveniles using a small sandblasting gun and compressed air at ~8.6 kg/cm^2. A different color of pigment was used to mark each group.

Prior to marking, the fish (mean fork length = 50.2 mm (SE = 2.9)) were removed from the hatchery pond, weighed, and transferred to a holding trough. About 500−750 fish were transferred by dip net from the holding trough and evenly distributed in a Plexiglas marking trough. The fish were immediately sprayed with one 8-s pass of the spray gun at 47.5 cm, the trough inverted, and the fish washed into a recovery trough leading to a hatchery pond.

Immediate mortalities from marking stress were enumerated prior to release (a minimum of 3 d after marking). A subsample of each marked group was retained for determination of the proportions which appeared well marked, poorly marked, or unmarked under ultraviolet illumination. A well-marked fish was defined as one which was determined to be marked upon initial examination under ultraviolet light. A poorly marked fish required examination under intense illumination (i.e. next to the ultraviolet light source) to confirm the presence of a mark. The same two observers were used during all phases of this study and periodically checked each

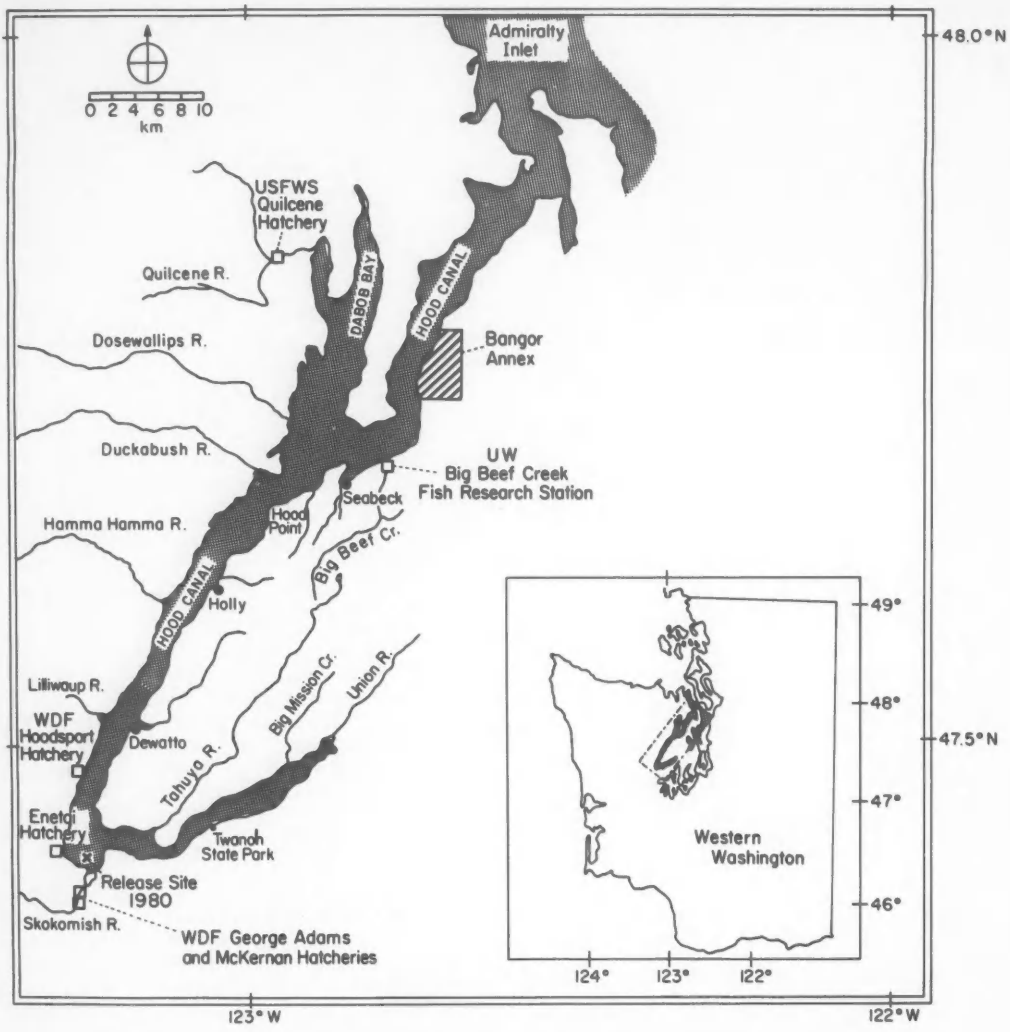

FIG. 1. Location of sampling area (Twanoh State Park to Hood Point) and release point (Enetai) in Hood Canal, Washington.

other's readings.

To estimate the effective release number (i.e. the number of fish with detectable marks), I determined the percentage of the marked fish that would not be detected during field mark evaluation. All field samples collected on the 3rd day of field sampling were separated into "marked" and "unmarked" categories and retained. It was assumed that analysis in the laboratory would yield 100% of the marked fish including the poorly marked. The percentages of marked fish not detected during the field mark examination did not differ (chi-square test; $P > 0.25$) from the laboratory-determined poorly marked percentages:

Group	Method	Detected marks or number well marked	Undetected marks or number poorly marked	Chi-square statistic
$M_{(1)}$	Field	52 (79%)	14 (21%)	0.2062
	Laboratory	184 (80%)	45 (20%)	
$M_{(2)}$	Field	18 (90%)	3 (10%)	0.6075
	Laboratory	88 (89%)	11 (11%)	

The effective release numbers were set equal to the well-marked category only, as established in the prerelease samples.

Recapture of Juvenile Chum Salmon

A floating 37-m-long beach seine and a 6.1-m-wide by 3.1-m-deep surface townet were used to collect marked chum salmon and assess their abundance. We used standardized beach seining and townetting techniques as used previously in a wide range of juvenile salmonid studies by the Fisheries Research Institute in this area. No attempt was made to estimate the midwater (>3 m) distribution of the juveniles; however, previous studies by Barraclough and Phillips (1978) have indicated that most juvenile chum salmon are located in the top 3 m of the water column. Townetting was confined to the 10-m depth contour because catches decline rapidly with increasing distance from shore but sampling any closer to shore would risk damaging the net. The catches on the 10-m-depth contour have been found representative of the offshore distribution sampled by the townet in Hood Canal (Bax unpublished data).

Salmonids caught were sorted, enumerated, and a subsample not exceeding 150 juvenile chum salmon taken from each beach seine and townet haul. The fish were killed with tricaine methanesulfonate (TMS) and viewed under ultraviolet illumination to determine the number marked. Small samples were counted. Large hauls were weighed in the field using a spring scale, and a numerical estimation of the total haul made from the average weight of the chum salmon in the subsample.

The manner in which loss from the population is estimated does not distinguish between mortality and emigration from the sampling area. The recapture data were insufficient to estimate the rate of emigration from the sampling area with precision; therefore, an overestimation of the maximum possible emigration from the sampling area was made. Application of this overestimate to the calculated daily loss from the sampling area will result in an underestimate of the true rate of mortality.

This overestimate was made on the assumption that all marked fish caught north or east of the Skokomish flats on the west shore would have migrated from the sampling area by the next day. The proportion of the population formed by these "emigrants" was estimated as the product of catch per beach seine set and the distance between sites east or north of the Skokomish flats (i.e. further than ±3.2 km from the release point, Enetai) compared to the total product of catch per set and distance for the west shore. This method provides an overestimate of the true emigration for two reasons. Firstly, it is unlikely that all marked fish caught away from the Skokomish flats and discounted from the calculation would in fact have migrated from the sampling area by the following day. Estimates of the migration speed of marked juvenile chum salmon of a similar size range released from hatcheries in Hood Canal were 9 and 7 km/d in April of 1977 and 1979, respectively, and 4 km/d in June of the same years (C. J. Whitmus, School of Fisheries, University of Washington, Seattle, WA 98195, unpublished data); the marked fish in this study would have to have migrated at 22 km/d, or greater, if they were all to have emigrated from the sampling area by the following day. Secondly, basing the proportions of marked fish on and off the Skokomish flats on only length of shoreline and catch per set does not take into account the extensive sublittoral habitat available to salmonids but not to the sampling gear on the Skokomish flats.

Estimation of Marine Mortality

The Jolly–Seber procedure used in this study follows that of Parker (1968), with the exception that the marked groups were assessed on the days following their release, rather than upon their return as adults. Additional terms have been added to Parker's equation to account for migration from the sampling area.

Notation

$M_{(x)}$	A distinct group of marked fish, where x is an integer from 1 to n, the number of groups released.
$N_{(x)i}$	Number of fish of a marked group, $M_{(x)}$, at any time i.
$n_{(x)i}$	An estimate of $N_{(x)i}$.
$S_{(x)}$	Fraction of a marked group, $M_{(x)}$, surviving the short-term effects of marking.
$V_{(x)}$	Fraction of a marked group, $M_{(x)}$, remaining in the sampling area after the emigration immediately upon release.
$v_{(x)ij}$	Fraction of group $N_{(x)i}$ not emigrating from the sampling area by time j.
$S_{(x)ij}$	Fraction of group $N_{(x)i}$ remaining at time j.
m	Long-term marking mortality which modifies the instantaneous natural mortality rate. In this study m is not estimated and thus the pooled effects of natural mortality and long-term marking mortality are indistinguishable.
q	Instantaneous daily natural mortality rate.

Model

The survival $S_{(1)ij}$ of a group of marked fish, $M_{(1)}$, released at time i, and enumerated at time k, can be computed from equation (3) of Parker (1968):

$$(1)\quad S_{(1)ij} = \exp -m(j-i)q = \frac{N_{(1)k}}{N_{(2)k}} \cdot \frac{N_{(2)i}}{N_{(1)i}} \cdot \frac{S_{(2)}}{S_{(1)}},$$

when a second, and distinct, marked group, $M_{(2)}$, is released at time j, a time intermediate between i and k. When migration from the sampling area is occurring in such a manner as to alter the probability of recapture of survivors of the two groups at time k, then additional terms are incorporated into the equation, which thus becomes:

$$(2)\quad S_{(1)ij} = \exp -m(j-i)q = \frac{N_{(1)k}}{N_{(2)k}} \cdot \frac{N_{(2)i}}{N_{(1)i}} \cdot \frac{S_{(2)}}{S_{(1)}} \cdot \frac{V_{(2)}}{V_{(1)}} \cdot \frac{1}{v_{(1)ij}}$$

With the exception of $v_{(1)ij}$ the components of this equation are ratios, and can be estimated without estimating the absolute value of the individual parameters.

Assumptions of the Model

1) The fraction of the fish surviving the short-term effects of marking, $S_{(1)}$ and $S_{(2)}$ is equal to unity for both groups.

Previous researchers using this marking technique reported no difference in mortalities between marked and unmarked juvenile chum salmon held in saltwater pens for 30 d after marking (S. Olsen, Washington State Department of Fisheries, Olympia, WA 98504, unpublished data). This assumption was reviewed by Parker (1968), who concluded that any losses due to marking were as a result of increased predator selectivity, and as such would be included in the long-term marking mortality coefficient m.

2) The long-term marking mortality coefficient m is equal for both groups.

The same marking technique was used by the same personnel to mark all groups used in this study. Provisional data indicates that the color of fluorescent pigment used does not influence predation on juvenile chum salmon (S. L. Schroder and K. L. Fresh, Washington State Department of Fisheries, Olympia, WA 98504, unpublished data).

3) The rate of natural mortality q is identical for both groups during the period $j-k$.

The groups of fish used in this study came from the same hatchery returns and were reared in the same environment. The second group was released at the center of the first group's distribution to ensure that similar environmental conditions were experienced by both groups. I assume the mortality schedules of both groups following release to be similar. It is possible that natural mortality is not constant during the period $i-k$, but in fact is higher for each group immediately following its release and subsequently declines. In this case $M_{(2)}$ will experience a higher mortality during the period $j-k$ than $M_{(1)}$, resulting in an overestimate of the survival of the first group $S_{(1)ij}$.

4) An identical fraction of both groups remains in the sampling area following the immediate emigration upon release.

If initial emigration is dependent on either the number of fish released or on the method of release, then this assumption would not be met. An estimate of the proportion of each group remaining in the sampling area on the west side will be made from a comparison of the east- and the west-side beach seine catches. As a further crude check on the validity of this assumption, daily loss from the larger group released directly from the hatchery will be compared with daily loss from the smaller group which was held in a net pen and transported by boat to the release point on the Skokomish River flats.

5) The two groups migrate from the sampling area at an identical rate during the period $j-k$.

Independent estimates of the mortality of $M_{(1)}$ will be made on consecutive days to test the validity of this assumption. Violation of this assumption will cause a trend in these estimates. A trend in these estimates could also result if assumptions 2 or 3 are not upheld.

6) The probability of recapture of marked individuals of any group remaining in the sampling area is proportional to the number of marked individual of that group remaining.

To satisfy this assumption, the sampling within the sampling area must be random or the distributions of the two groups must be identical. Random sampling would have been impractical given the sampling gear and its method of deployment. The similarity in the distributions of the groups in the sampling area, as indicated by recaptures, will be a measure of the validity of this assumption.

Application of assumptions 1 and 4 to equation (2) reduce it to:

$$(3)\quad S_{(1)ij} = \frac{N_{(1)k}}{N_{(2)k}} \cdot \frac{N_{(2)j}}{N_{(1)i}} \cdot \frac{1}{v_{(1)ij}} .$$

This equation consists of two population ratios, whose product changes linearly with mortality of the first population taking place between the times of the two releases ($i-j$), modified to account for emigration of the first group from the sampling area.

The estimate of each variable in equation (3) has an associated statistical variance. The estimate of the size of each group at release ($N_{(1)i}$ and $N_{(2)j}$) includes a correction for incomplete or poor mark retention. The associated variance is estimated from the binomial approximation. The variances of the estimates of population sizes at time of recapture ($n_{(1)k}$ and $n_{(2)k}$) are the sum of individual variances at each site. At sites where no repeated sampling occurred, and thus no estimate of variance was available, the mean of the variances from the other sites was assumed representative. The variance of the estimate of the fraction not emigrating from the sampling area ($v_{(1)ij}$) was estimated as the variance of the slope of a linear regression run on the fraction remaining by days since release. The variance of the survival estimate was then estimated from these individual variances using the delta method (Seber 1973, p. 7).

Experimental Design

Three distinct marked groups, $M_{(1)}$, $M_{(2)}$, and $M_{(3)}$, were released on days $t = 0$, $t = 2$, and $t = 4$, respectively. Separate estimates of the fraction remaining in the sampling area of $M_{(1)}$ from day 0 to day 2 were made from recaptures of $M_{(1)}$ and $M_{(2)}$ on days 3, 4, and 5. An estimate of the fraction of $M_{(1)}$ remaining from day 0 to day 4, and an estimate of the fraction of $M_{(2)}$ remaining from day 2 to day 4 were made from the recaptures of the three groups on day 5. Recaptures used in these estimates were the unweighted total recaptures of each marked group in the sampling area.

This design can be summarized:

	Days (t)					
	0	1	2	3	4	5
Releases and recaptures	$N_{(1)0}$			$n_{(1)3}$	$n_{(1)4}$	$n_{(1)5}$
			$N_{(2)2}$	$n_{(2)3}$	$n_{(2)4}$	$n_{(2)5}$
					$N_{(3)4}$	$n_{(3)5}$
Fraction remaining				$S_{(1)0,2}$	$S_{(1)0,2}$	$S_{(1)0,2}$
						$S_{(1)0,4}$
						$S_{(2)2,4}$

These estimates of the fraction remaining were calculated with the assumption that the fraction of $N_{(x)i}$ not emigrating from the sampling area in the period $i-j$ was equal to unity

TABLE 1. Effective release numbers of marked groups released into southern Hood Canal from May 18 to May 22, 1980, and the number recaptured from each group in the westside nearshore zone. The estimated standard error is in parentheses under each value.

	Day (t)					
Group	0	1	2	3	4	5
$M_{(1)}$	232 053	53	111	327	68	178
	(11 765)			(90)	(11)	(25)
$M_{(2)}$			50 775	152	39	91
			(1 943)	(31)	(7)	(12)
$M_{(3)}$					15 629	64
					(172)	(7)

TABLE 2. Estimated average daily mortality for marked fish released into southern Hood Canal in May, 1980. The estimated standard error is in parentheses under each value.

Groups used in estimate	Time between release of groups (d)	Estimated on day	Instantaneous daily loss	Estimated maximum emigration	Instantaneous daily mortality
$M_{(1)}/M_{(2)}$	2	3	0.38	0.08	0.34
			(0.12, 0.95)	(0.03)	(0.15, 0.64)
$M_{(1)}/M_{(2)}$	2	4	0.49	0.08	0.46
			(0.30, 0.83)	(0.03)	(0.26, 0.81)
$M_{(1)}/M_{(2)}$	2	5	0.42	0.08	0.38
			(0.26, 0.67)	(0.03)	(0.28, 0.50)
$M_{(2)}/M_{(3)}$	2	5	0.41	0.20	0.31
			(0.26, 0.62)	(0.04)	(0.15, 0.54)
$M_{(1)}/M_{(3)}$	4	5	0.42	0.25	0.35
			(0.34, 0.53)	(0.02)	(0.27, 0.46)

($v_{(x)ij} = 1.0$). The survival estimate was then calculated incorporating the estimated maximum emigration. The estimate of $v_{(x)ij}$ was corrected for the reduced population (the mean of $N_{(x)i}$ and $N_{(x)j}$) that it was operating on. In this manner $v_{(x)ij}$ was estimated as the fraction of the original population remaining at time j. To facilitate comparison of survivals estimated over different time periods, the results are reported as the instantaneous daily mortality rate.

Results

Nine-hundred and nineteen marked fish were recaptured in the sampling area during the 3-d period from which estimates of mortality were to be made (Table 1). The initial estimates of the mean daily loss to the population ranged from 38 to 49%, but the confidence intervals were broad (Table 2). When these values were adjusted by the estimated maximum emigration of the first marked group in each comparison, the calculated mean daily mortality rate was 31–46% (Table 2).

The estimated emigration does not include the initial dispersal upon release, which was assumed equal for all groups. Under this assumption the estimates of daily loss would be unaffected by the extent of the dispersal. Considerable dispersal did occur (Fig. 2 and 3). The proportions of the beach seine recaptures of $M_{(1)}$, $M_{(2)}$, and $M_{(3)}$ recaptured on the east shore were 0.36, 0.29, and 0.37, respectively, which suggests that this assumption was valid. However, sampling on the east shore did not cover the geographic distribution of the marked fish and, consequently, a further check on the validity of this assumption was made. The daily loss of $M_{(1)}$ from the sampling area was estimated from the recaptures of $M_{(1)}$ and $M_{(3)}$ on day 5, and compared with the daily loss of $M_{(2)}$, estimated from recaptures of $M_{(2)}$ and $M_{(3)}$ on the same day. $M_{(1)}$ was a large group released directly from the hatchery, whereas $M_{(2)}$ was a smaller group, which had been held in a saltwater pen for 2 d before being transported to the Skokomish River flats and released. The estimates of mean daily loss from the two groups were very similar (Table 2), indicating that the initial dispersal was not markedly different for the two groups.

A second way in which emigration can affect the mortality estimates is if the groups migrate at a different rate from the sampling area when both groups are present, but after the initial dispersal. The estimated emigration rate of $M_{(2)}$ was greater than that of $M_{(1)}$ in the 2 d following its release (Fig. 4), suggesting that assumption 5 was not valid. However, the mean mortality estimates were consistent over the 3-d period indicating that the assumption may in fact have been upheld, and that the estimates of emigration were overestimates as suggested in Materials and Methods.

The wide confidence bounds associated with the estimates of mortality preclude emphasizing individual values. The consistency of the estimates is surprising for this reason, and suggests that the variance estimates may have been conservative.

The consistency of the estimates of the daily mortality rate of $M_{(1)}$ from recaptures on days 3, 4, and 5 was the anticipated result if $M_{(1)}$ and $M_{(2)}$ suffered similar losses from long-term marking mortality, suffered similar rates of natural mortality from day 3 to day 5, and had similar rates of emigration in that period. This suggests that assumptions 2, 3, and 5 were

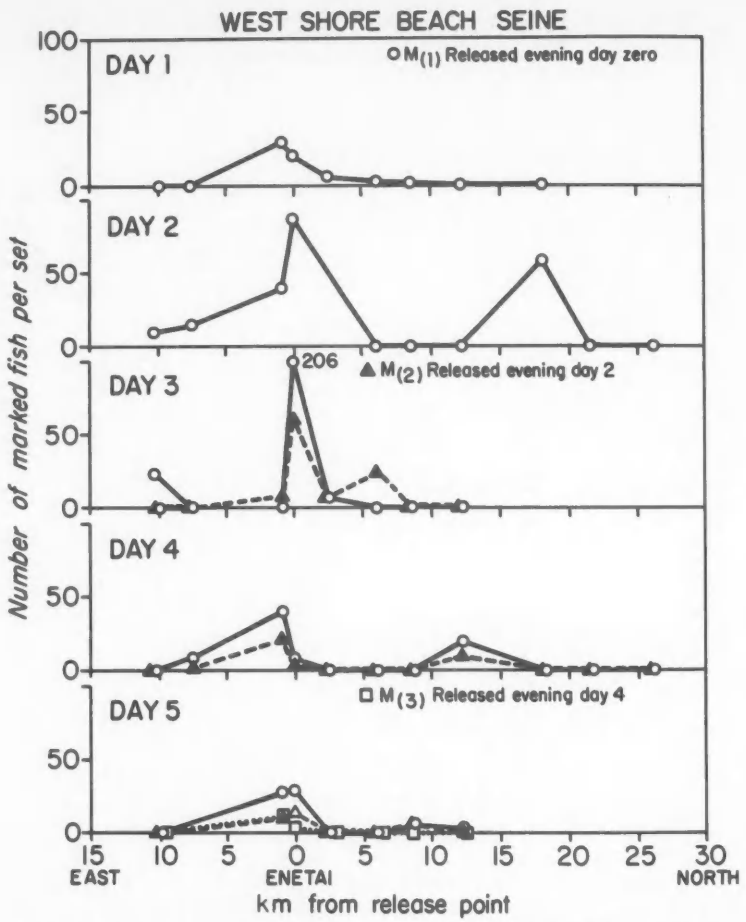

FIG. 2. Distribution of recaptures of marked fish with the beach seine on the west side of Hood Canal.

reasonable. The similarity in the estimates of daily mortality for $M_{(1)}$ and $M_{(2)}$ was anticipated if the initial losses of marked fish from the sampling area was comparable for both groups. Thus assumptions 1 and 4 appear to have been upheld.

The sixth and final identified assumption of this model was that individual fish from any marked group remaining in the sampling area had an equal probability of recapture. The sampling was nonrandom and this assumption is thus dependent upon equal distributions of the groups in the sampling area. On all 3 days when more than one group was present in the sampling area the main peak of recaptures occurred within 1 km of the release site for all groups (Fig. 2). A second, and smaller, peak of recaptures occurred further north on days 4 and 5 for all groups. On day 3 there was a second peak to the north of the release site for $M_{(2)}$, but not for $M_{(1)}$. With the possible exception of the 3rd day the assumption of an equal distribution of the groups within the sampling area appears to have been satisfied. An anonymous reviewer expressed concern that the sampling design would lead to the recapture of proportionately more fish from a peaked than from a more diffuse distribution, when the mode of both groups' distribution was close to the center of the sampling area. If this had been the case, then the overestimate of emigration, which was calculated as the proportion of the marked fish from each group away from the Skokomish River flats (the mode) would compensate for any decreased probability of recapture of fish from the more diffuse distribution.

Discussion

There are few prior studies with which to compare these estimates of early marine survival. Parker (1962), assuming "ecological similarity" between pink and chum salmon, estimated that the survival of juvenile chum salmon during

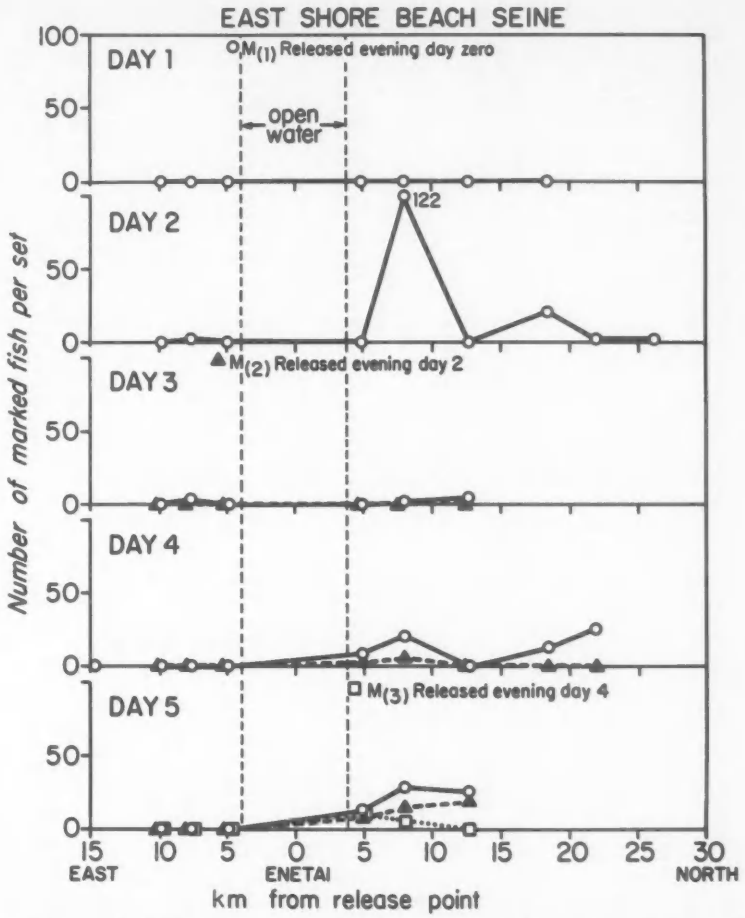

FIG. 3. Distribution of recaptures of marked fish with the beach seine on the east side of Hood Canal.

the 5-mo coastal period was 5.45%. In a later study, Parker (1968) estimated that from 2 to 4% average daily loss occurred to a pink salmon population during the initial 40-d period of sea life. Results from other research suggesting the importance of environmental and other variables during the early marine phase on the return of adult chum salmon in Puget Sound (Gallagher 1979) and adult pink salmon in other areas (Vernon 1958; Gilhousen 1962; Jones 1980) support the concept of the early marine environment being a critical period in the life history of chum salmon. The estimated average daily mortality for the population in this study was between 31 and 46%. The estimated daily mortality did not change over the 4-d period of the study. These estimates are an order of magnitude higher than estimates for pink salmon over a 40-d period subsequent to saltwater entry (Parker 1968). Several factors, in addition to the different species and area studied, may have contributed to this difference.

Fish in this study comprised a different portion of the total population than those in Parker's studies. Pink salmon fingerlings marked in Parker's studies were seined from two areas in each year. The initial marking was on fish seined from an area 0–8 km from the mouth of the Bella Coola River in 1964, 8 km from the river mouth in 1963, and ~100 km from the river mouth in 1962 (Parker 1965, 1968). The second area seined was ~100 km from the mouth of the Bella Coola River in 1964, and ~125 km from the river mouth in 1962 and 1963. Parker does not indicate whether the fish were seined from the shore, or in open water, or both. I restricted the data analysis in this study to fish recaptured from the shore on the west side of Hood Canal, the side of the Canal from which the fish were released. The bulk of the recaptures came from sampling sites less than 1 km from the release point. Thus, the mortality estimates in this study apply to that portion of the population remaining close to the release site in the first 4 d

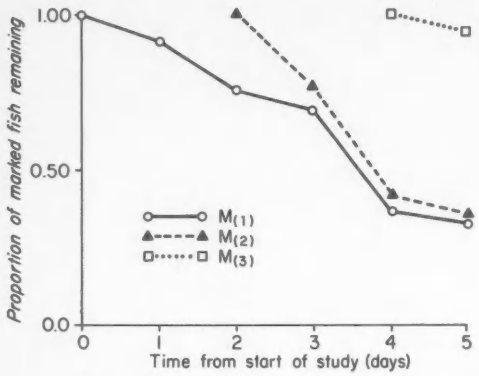

FIG. 4. Estimated maximum emigration from the Skokomish River Flats.

after release. The mortality of the entire population may be other than estimated from this portion. The mortalities estimated in Parker's studies apply to that portion of the population in the process of, or having already successfully undergone, movement off the beach.[2]

An important difference between the two studies is that Parker's studies averaged daily mortality rates over a 40-d period. This study averaged daily mortality rates only over a 4-d period. Parker (1968) notes that the "average rates [of mortality] may be misleading" over a 40-d time period. A higher mortality in the first few days would have been masked.

The juvenile salmon used in this study may have been especially susceptible to predation. Popov (1953 cited by Kanayama 1968) pointed out that hatchery-reared chum salmon fry lack the adaptability to changing natural conditions in comparison with wild fry of the same size. Kanayama (1968) found that wild chum salmon fry were already conditioned to respond to potential predators during downstream migration, unlike hatchery fry. Bams (1979) found the fry-to-adult survival of pink salmon to be suppressed by 6–8% in the case of hatchery fish when compared with naturally produced fish. Bams went on to say that this difference in ocean survival may be associated with a delayed mortality of inferior stock, "artificially kept alive in the hatchery."

An additional effect of hatchery releases on juvenile salmon is associated with the attraction of predators to the release sites. Larsson and Larsson (1975) found that the abundance of burbot (*Lota lota*) increased within 50 m of the release point of juvenile Atlantic salmon (*Salmo salar*) as releases began. Similar increases in the abundance of predators have been observed at the release point of hatchery-reared juvenile chum salmon in Big Beef Creek (C. J. Whitmus, School of Fisheries, University of Washington, Seattle, WA 98195, personal communication) and in Prince William Sound (R. T. Cooney, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, personal communication). Thus, there are indications that the high mortality estimated in this study, compared to that estimated by Parker (1968), may be partly attributable to the repeated releases of hatchery fish. The sampling design, which estimated the mortality of those fish remaining near the release site over a 4-d time period, would have accentuated any such differences. Because of these differences in populations and time periods studied, the two studies are not directly comparable; however, the large disparity in estimates from the two studies suggest that the average rates of mortality calculated by Parker (1968) are indeed average rates over a period of highly variable mortality.

[2]Parker (1965) observed that salmon fry were very abundant along the shore close to the mouth of the Bella Coola River, but were "generally off the beach" 2 wk later and 60 km from the river mouth.

Acknowledgments

The Point No Point Treaty Council provided the fish for this study, facilities for their marking, and helped with the field sampling. Mr C. J. Whitmus organized the marking of the fish and their recovery, and provided exceptional assistance throughout all stages of the study. The research personnel of the Big Beef Creek Fish Research Station gave unstintingly of their assistance in the field recovery of the marked fish and provided many helpful suggestions. Dr D. G. Chapman provided valuable advice on the statistical procedures used. Earlier drafts of this paper were critically reviewed and improved by Dr E. O. Salo, Dr R. L. Burgner, Dr D. R. Gunderson, Mr C. A. Simenstad, Mr A. F. Gallagher Jr., and two anonymous reviewers. This project was supported by the Washington Sea Grant Program, the National Marine Fisheries Service, and the Washington State Department of Fisheries.

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Unionid Growth Curves Derived from Annual Rings: A Baseline Model for Long Point Bay, Lake Erie

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MCCUAIG, J. M., AND R. H. GREEN. 1983. Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. Can. J. Fish. Aquat. Sci. 40: 436–442.

Growth curves for *Lampsilis radiata* and *Anodonta grandis* collected in July 1981 at three stations in Long Point Bay, Lake Erie, were determined based on measured lengths at annual winter shell rings. A Walford Plot technique was used to convert annual growth-in-length increments to length vs. age growth models. For the two species, we used simulated baseline and environmental impact data to illustrate the use of baseline growth models in testing for long-term environmental deterioration.

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À partir des longueurs au moment de la formation d'anneaux annuels d'hiver sur la coquille, nous avons établi les courbes de croissance de *Lampsilis radiata* et d'*Anodonta grandis* recueillis en juillet 1981 à trois stations de la baie Longue-Pointe (lac Érié). Le tracé de Walford a été utilisé pour convertir les augmentations annuelles de croissance en longueur en modèles de croissance en longueur vs. âge. Nous avons fait appel, pour les deux espèces, à une simulation de données de référence fondamentale et d'impact sur l'environnement dans le but d'utiliser le modèle de croissance de base pour vérifier la détérioration à long terme de l'environnement.

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IN temperate latitudes bivalve mollusks undergo seasonal variations in growth that are recorded in their shells as winter growth rings. Use of molluscan shells as records of past and present-day environments has been recently reviewed and thoroughly documented by Rhoads and Lutz (1980). Growth rate as an indicator of environmental impact has been largely neglected.

Bivalve growth rates are known to vary with environmental conditions. Oxygen supply, turbidity, substratum, temperature, light, depth, population density, food supply, and strong-water agitation all influence growth rates in bivalves (Hallam 1965; Stansbery 1967). Rapid temperature fluctuations are an important cause of pseudoannuli, or growth interruptions not related to normal winter growth cessation, and the number produced is proportional to the temperature instability of a body of water (Stansbery 1967). Pseudoannuli, however, are reliably identified in unionids as thin and incomplete bands, differing in color and texture, and lacking in the periodicity of yearly bands (Isely 1914; Coker et al. 1920; Stansbery 1961; Negus 1966). Recent methods for reading bands from sectioned shells (Rhoads and Lutz 1980) can replace, or validate, analysis of bands on the shell external surface.

Because growth history of bivalves can be determined from growth banding, change of growth rate caused either by short-term or long-term environmental change can be discerned. Kennish (1976) measured the effects of thermal effluent on the growth of the bivalve *Mercenaria mercenaria* and found a reduction in daily summer growth increments of 10–30% due to excessively high water temperatures. On the other hand, Negus (1966) observed increased growth of *Anodonta anatina* because of a heated effluent.

Unionids with wide geographic distribution such as *Lampsilis radiata* and *Anodonta grandis* are valuable research organisms because much taxonomic, zoogeographic, and ecological information on them already exists, and because growth rate differences related to natural environmental variability can be identified. Long Point Bay, which supports a large fish spawning community and important waterfowl populations, is a valuable study site. It is a popular commercial and sportfishing area, heavily cottaged, and potentially vulnerable to impact from the nearby Nanticoke industrial development area. Here we derive baseline growth rates from annual growth rings for *L. radiata* and *A. grandis*, to illustrate use in future tests of environmental change.

Methods and Materials

Sampling for live clams was done by SCUBA in July 1981 at four stations which are shown in Fig. 1. Clams were detected by sight and touch; all sizes were sampled. Abun-

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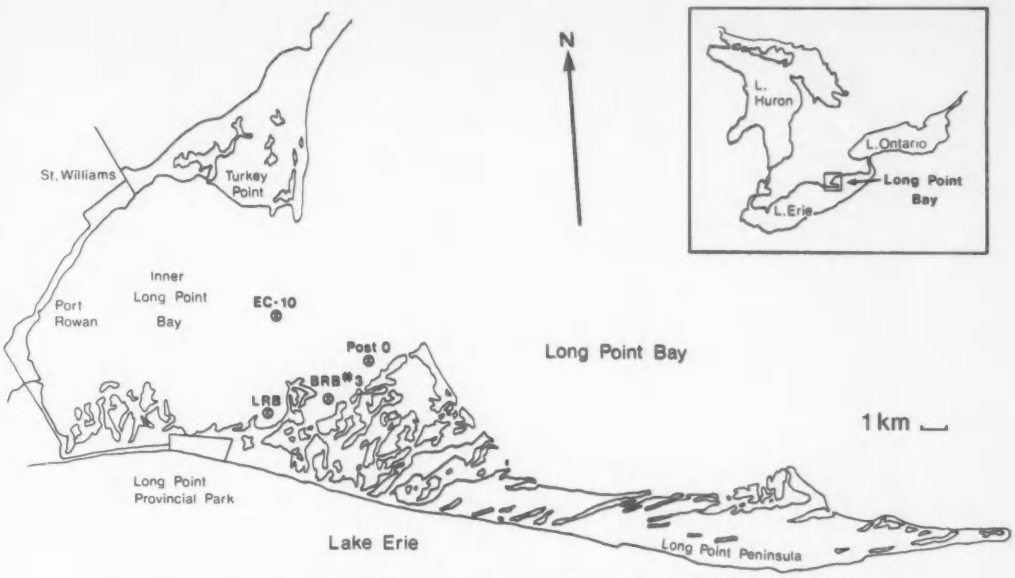

FIG. 1. Long Point Bay showing the four sampling stations. Inset shows location of bay in Lake Erie.

dances of the three most common species varied among the stations (Table 1). *Elliptio dilatata* was abundant at only one station; therefore, we restricted our study to *L. radiata* and *A. grandis*.

Lengths at annual winter rings were measured with vernier calipers and recorded separately for each species and station. The annularity of the measured rings is highly probable. We have not done marking studies at Long Point Bay, but such studies on *Anodonta* in a Manitoba lake (Green unpublished data), a Quebec lake (G. L. Mackie, University of Guelph, personal communication), and the River Thames in England (Negus 1966) indicate annual (winter growth cessation) rings. Unionid species differ in separation and clarity of annual rings on the shell external surface — for example, *Elliptio* rings are difficult to read (Strayer et al. 1981) whereas *Anodonta* rings are especially clear and *Lampsilis* almost as clear. On our specimens the spacing of the presumed annual rings on the external shell surface was very regular and consistent from individual to individual within each species.

Early workers were concerned with variable darkness of lines on the shell surface, and doubted the reliability of aging methods based on "annular rings" of unionids (e.g. Lefevre and Curtis 1912). However, subsequent workers (Coker et al. 1920; Negus 1966) found that annual rings on the shell surface, verified by examination of internal bands in shell sections, are easily distinguished from "disturbance rings" in that annual rings have a closely packed stop/start pattern (and are therefore darker) whereas disturbance rings are lighter and thinner single lines. There is, of course, greater difficulty when working with shallow-water marine bivalves, especially at lower latitudes; a less extreme seasonal temperature cycle combined with tidal cycles of various periodicities results in weaker annual rings with many non-annual rings between them. However, for lentic unionids Chamberlain (1931) cites Isely (1914) as concluding "from his study of some 900 specimens of North American species of fresh-water mussels which he tagged and subsequently recovered ... that the winter rings ... are usually sufficiently regular and definite to be used as indicators of age." Chamberlain himself concludes, from his work with *Lampsilis* species in Minnesota and Wisconsin lakes, that "Considering all of the data obtained from over 1,100 specimens, the application of the annual-ring method to growth studies of fresh-water mussels seems both reliable and practical, judging from the uniformity of the growth curves and the ease with which these measurements may be made on the great majority of shells."

In any case the only necessary assumption for our objectives and for the statistical methods proposed and illustrated here is regularity, not annularity. Certainly the rings are regular, on the shell external surface and also in thin sections (after Clark 1980) as illustrated in Fig. 2. If, for example, the rings were semiannual rather than annual, then the statistical tests which follow would be unaffected. If there were also some added error due to disturbance rings being sometimes

TABLE 1. Number of clams collected at the four stations in Long Point Bay.

Species	Stations			
	Post 0	EC-10	BRB#3	LRB
Lampsilis radiata	24	17	7	17
Anodonta grandis	9	17	10	3
Elliptio dilatata	20	1	1	0

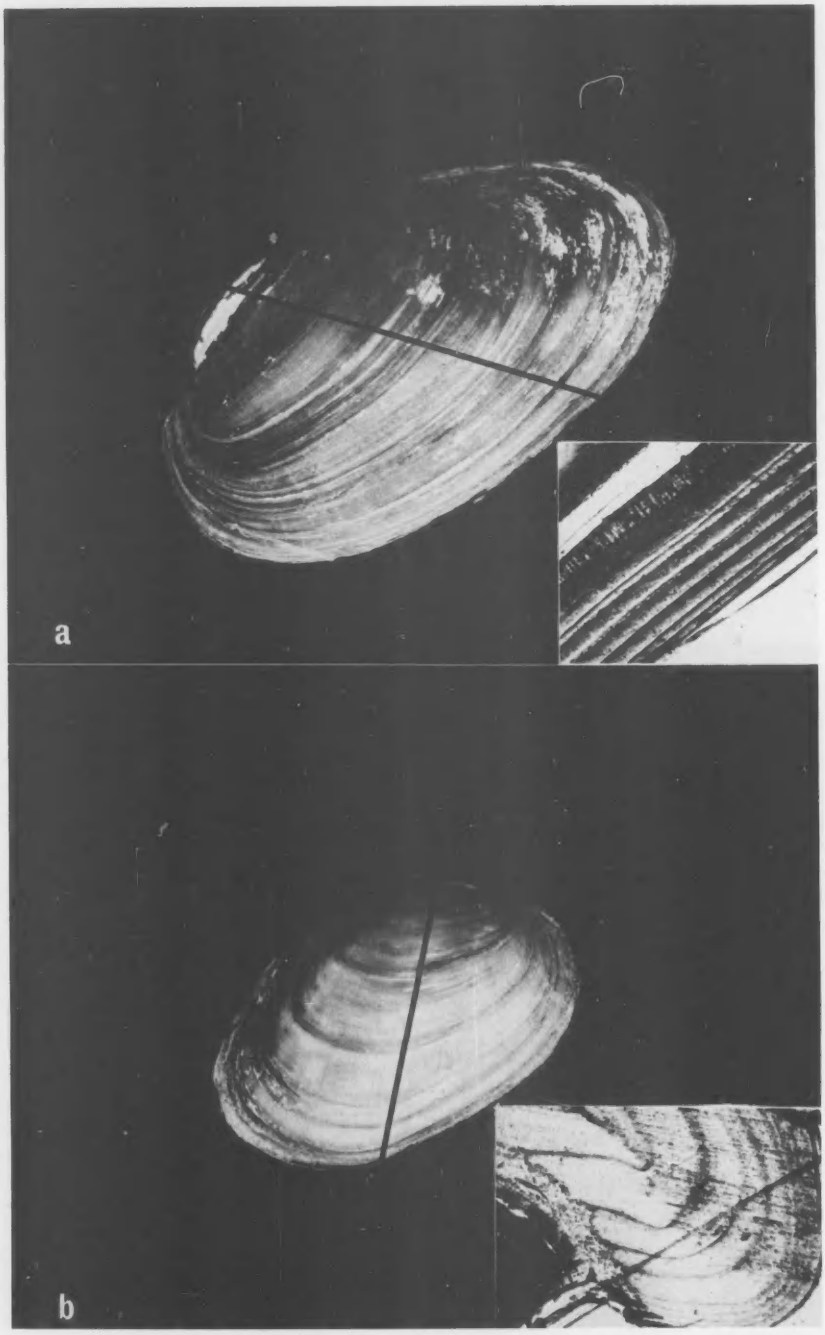

FIG. 2. Thin sections of (a) *Anodonta grandis* and (b) *Lampsilis radiata* verify age by annual growth rings.

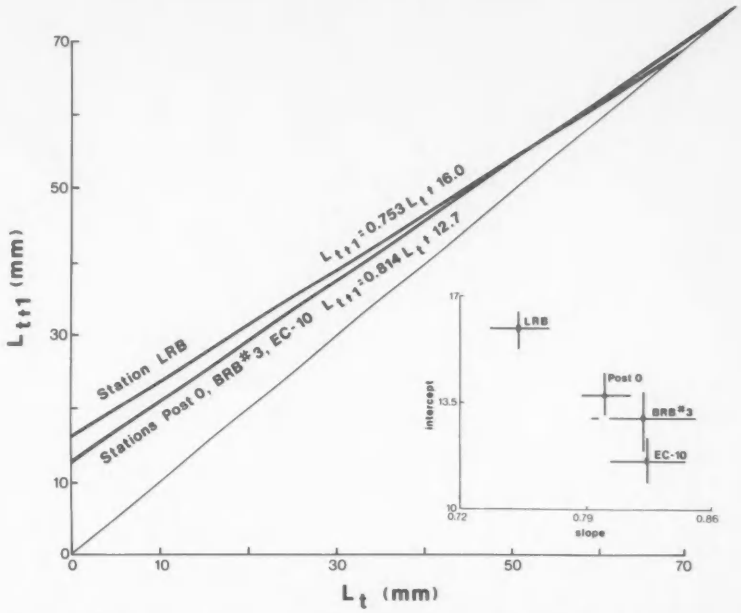

FIG. 3. Walford Plots for *Lampsilis radiata* of lengths at consecutive winter rings, and inset of intercepts vs. slopes ± SE, showing differences between station LRB and stations Post 0, BRB#3, and EC-10.

treated as annual rings, then the tests would be biased but conservatively so (i.e. the error variance would be inflated and any real change in growth rates would be more difficult to detect).

We have used the "Walford Plot" method of Ford (1933) and Walford (1946) as applied by Green (1973), to describe the growth data and to test hypotheses. A Walford Plot is a difference equation representation of the data as a "length next year (L_{t+1}) versus length this year (L_t)" bivariate plot. A linear Walford Plot model $L_{t+1} = bL_t + a$ implies the Von Bertalanffy growth model $L_t = L_\infty(1 - e^{-Kt})$, assuming $L_O = 0$. The parameters are related as $L_\infty = a/(1 - b)$ and $K = -\ln b$, where L_∞ = asymptotic final size, K = instantaneous growth rate at $t = 0$ expressed as a fraction of L_∞, b = fraction of total growth remaining after the 1st year, and a = 1st year's growth. A nonlinear Walford Plot would imply some other member of this family of growth curves which includes the Gompertz and logistic models (Richards 1959; Kaufman 1981). All of these models have corresponding Walford Plot models. However, the Von Bertalanffy model sufficed for the data considered here.

Our analysis and hypothesis-testing of growth rate parameters use classical linear additive model statistics (e.g. analysis of covariance) on the Walford Plot models rather than analysis based on index-type derived variables (e.g. Richardson et al. 1980; Kaufman 1981). Our approach applies a standard method (analysis of covariance) to a simple linear regression model ($L_{t+1} = bL_t + a$) which relates the original measured variables (lengths at winter rings), rather than complex derived variables, to each other. We believe that this approach creates fewer problems with underlying assumptions, and with ambiguities in interpretation of results. A possible extension of this approach is discussed later.

Our data base is of sufficient size for our purposes here. Each of the clams in Table 1 yields about 8 points on the Walford Plot, and the minimum error degrees of freedom in any test is 172. Rings can be thought of as nested within clams, and our statistical analysis understood as using an error df which pools among-clam and among-rings (within-clams) variation. Even if the more conservative approach of using only among-clam variation as the error term had been used, there would have been a more-than-adequate minimum of 69 error df, and similar results. In fact we would caution against overreplicating in such studies, which could lead to "statistical significance" of trivially small (re — biological importance) growth rate differences. Replication should be sufficient to provide robustness against failures of assumptions in the tests (see Green 1979), and then chosen to provide the Type I and Type II error rates wanted for the magnitude of growth rate change being detected.

Analysis of covariance indicated that the null hypothesis of similar slopes for the four stations should be rejected ($F(1, 416$ df$) = 4.84$, $P < 0.05$). *Lampsilis radiata* at station LRB had a higher growth rate (inset, Fig. 3). Station LRB was closest to shore and less than 1 m deep whereas stations Post 0, EC-10, and BRB#3 were 2−4 m deep. We also noted the reduced numbers of *A. grandis* at this site. Because of its biological and environmental differences from the other

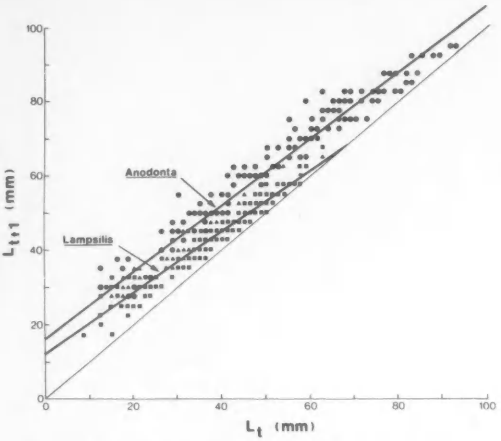

FIG. 4. Walford Plots of lengths at consecutive winter rings for the three stations pooled for *L. radiata* (■) and *A. grandis* (●). (▲ is overlap.)

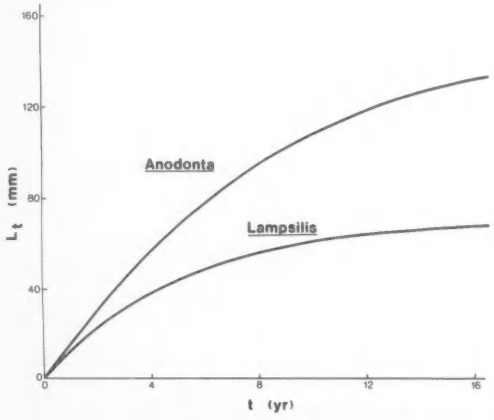

FIG. 5. Baseline growth curves for *L. radiata* and *A. grandis*.

stations we dropped station LRB from the remaining analysis.

The Walford Plot growth equations for the three stations pooled (Fig. 4) are as follows:

$$L.\ radiata \quad L_{t+1} = 0.814L_t + 12.7$$
$$A.\ grandis \quad L_{t+1} = 0.894L_t + 16.9.$$

Analysis of covariance indicated that the slopes and intercepts do not differ ($P > 0.05$) among the three stations, for either species.

The Von Bertalanffy growth model was used to represent the baseline growth curves (Fig. 5) for the two species:

$$L.\ radiata \quad L_t = 68.6(1 - e^{-0.205t})$$
$$A.\ grandis \quad L_t = 158.6(1 - e^{-0.113t}).$$

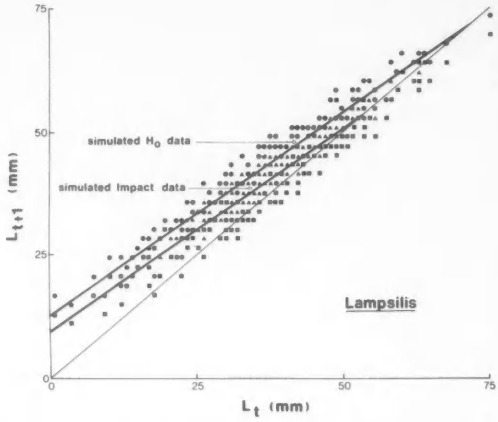

FIG. 6. Walford Plots of lengths at consecutive winter rings for *L. radiata* simulated H_O data (●) and simulated H_A data (■). (▲ is overlap.)

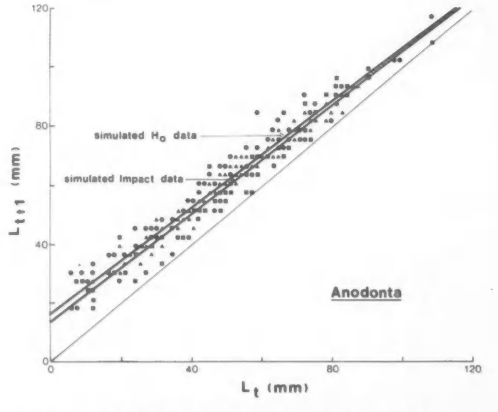

FIG. 7. Walford Plots of lengths at consecutive winter rings for *A. grandis* simulated H_O data (●) and simulated H_A data (■). (▲ is overlap.)

Simulation of H_O (Baseline) and H_A (Impact) Data

For *L. radiata* the H_O data were simulated to have the same statistical properties as the Walford Plot data shown in Fig. 4, namely $L_{t+1} = 0.814L_t + 12.7 + \epsilon$ where ϵ has approximately the same normal distribution of errors about the regression line ($= \sqrt{\text{error mean square}} = \sqrt{5.49} = 2.34$). The H_A data were simulated to represent a hypothesized impact that lowered the amount of 1st-year growth (the intercept a) but did not change the fraction of growth remaining to be done (the slope b). Thus a different asymptotic size would be approached at the same rate, with growth rate lower at all ages. These data had the same properties as the H_O data except that the 1st year of growth was lowered by 3.5 mm to

a = 9.2 mm, yielding the Walford Plot growth equation $L_{t+1} = 0.814L_t + 9.2$.

Similarly for *A. grandis* the H_O data were simulated to have the same statistical properties as the Walford Plot data shown in Fig. 4, namely $L_{t+1} = 0.894L_t + 16.9 + \epsilon$ (with $\epsilon = \sqrt{\text{error mean square}} = \sqrt{13.35} = 3.65$). The H_A data were simulated to represent the effect of a hypothesized impact, but in this case the impact lowers the amount of 1st year growth by 3.5 mm and increases the fraction of growth remaining to be done so as to yield the same asymptotic size L_∞ = 158.6 mm (Fig. 5), which yields a Walford Plot growth equation of $L_{t+1} = 0.916L_t + 13.4$. Here the effect of the impact is to lower initial growth rate but to compensate for that decrease by retaining a higher fraction of that growth rate in older ages.

Testing H_A (Impact) Data Against H_O (Baseline) Data

We used analysis of covariance to test for differences between simulated data and the actual 1981 data. As expected, the simulated H_O *L. radiata* data did not differ from the actual 1981 data in either slope or intercept ($P > 0.05$). The simulated H_A data were tested against the simulated H_O data and, as expected, slopes were similar ($P > 0.05$) whereas intercepts differed ($P < 0.01$) as shown in Fig. 6.

Also as expected, the simulated *A. grandis* H_O data did not differ in slope or intercept from the actual 1981 data ($P > 0.05$), and against it the simulated H_A data were tested. The slopes of the two models differed ($P < 0.05$), thus rendering a test of intercepts meaningless, and demonstrating that the two growth equations are different as shown in Fig. 7.

Discussion

We have shown how growth rate parameters can be used to test hypotheses about change in environment, e.g. long-term increase or decrease in temperature, or presence of a pollutant. To do so we simulated a biological response to impact consisting of about 29% decrease in growth rate, in one case throughout the life span and in the other case a maximum effect at the beginning of life. Such a magnitude of decrease is consistent with observed variation in adult size in *L. radiata* (Green 1972) and in growth rates in *A. grandis* (Green unpublished data) over a wide range of environments. The error distribution was based on that observed for our Long Point Bay material. The results of the tests, using our recommended methods, agree with the properties of the simulated data.

If absolute age of a live clam can be estimated, then so can year of death and so can the year in which any particular band was formed. It is then possible to relate growth to yearly environmental variation (e.g. Negus 1966; Richardson et al. 1980; Jones 1981). Unionids can concentrate trace elements, and the shell is an exact chronology of chemical events (Tevesz and Carter 1980). Chemical concentrations in bivalve shell sections, separated at various growth bands, can be analyzed and related to specific years (i.e. specific events). This has not been our purpose here, but we plan such studies utilizing unionids and other bivalves, and feel that extensions of the difference equation (i.e. Walford Plot) approach can provide a better statistical treatment of such data than that in published work to date. For example, the parameter a, the intercept, can be treated as a function of the yearly varying environmental parameter (call it X) that is hypothesized to modify growth rate. If a linear function of the deviation of X from its mean ($X' = X - \bar{X}$) during that time period is used, then we have the simple and statistically tractable model $L_{t+1} = a + bL_t + cX'$. A test of the null hypothesis H_O: "$c = 0$" corresponds to a test of H_O: "No linear model relationship between year-to-year variation in growth rate and year-to-year variation in environmental parameter X." The sequential yearly observations are of course not randomly allocated replicate observations (in time), as the simple covariance model implies, but this is equally true of the usual statistical treatment of such data. If this is a concern, then our proposed model could be analyzed as a time-series model which would take into account any autocorrelation between years.

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Genetic Differentiation in the Face of Gene Flow: A Study of Mussel Populations from a Single Nova Scotian Embayment

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There are significant genetic differences among populations of the blue mussel, *Mytilus edulis*, from six localities in St. Margaret's Bay, N.S., Canada, despite the presence of gene flow. The populations are differentiated into two groups, those at the head of the bay where ambient conditions fluctuate widely during the year, and those at the mouth of the bay where conditions (particularly salinity) fluctuate to a lesser degree. Three isoenzyme loci, i.e. leucine aminopeptidase 1, peptidase 2, and phosphoglucose mutase, show a clear shift in the predominant frequencies, from slow migrating alleles at the mouth of the bay to faster migrating alleles at the head of the bay. This shift is a microgeographic parallel of the pattern we observed in 1980 on a macrogeographic scale. A genetic comparison of these populations with those studied previously shows that allele "populations" cluster according to their environment and not according to geographical proximity. We conclude that differences in allele frequencies among localities index heterogeneity among environmental conditions, and that the sensitivity to environmental selective forces varies from locus to locus.

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Il existe, entre les populations de moules bleues, *Mytilus edulis*, de six endroits de la baie St. Margaret, en Nouvelle-Écosse (Canada), des différences génétiques marquées, en dépit d'un échange de gènes. Ces populations se séparent en deux groupes, celui de la tête de la baie où les conditions ambiantes varient grandement au cours de l'année et celui de l'embouchure où les fluctuations (surtout de la salinité) ne sont pas aussi fortes. Trois loci d'isoenzymes, soit la leucine aminopeptidase 1, la peptidase 2 et la phosphoglucose mutase, montrent un glissement net des fréquences prédominantes, depuis des allèles à migration lente à l'embouchure à des allèles à migration plus rapide à la tête de la baie. Ce glissement se compare, à échelle microgéographique, à celui qui avait été observé en 1980 à échelle macrogéographique. Une comparaison génétique de ces populations avec celles étudiées antérieurement démontre que les « populations » d'allèles se groupent selon leur environnement et non leur rapprochement géographique. Nous concluons que les différences de fréquences alléliques d'un endroit à l'autre reflètent l'hétérogénéité des conditions ambiantes et que la sensibilité aux agents de sélection varie d'un locus à l'autre.

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THE response of animal populations to changes in their surroundings results from physiological adaptation which may or may not involve changes in genetic constitution. Gause (1947) postulated that animals subject to highly variable environments are likely to exhibit higher genotypic plasticity but lower initial phenotypic adaptation than those inhabiting stable environments. Such features would suggest that various species offer different properties as indices of environmental quality, as well as different inherent capacities for deliberate selective modification.

In an earlier paper (Gartner-Kepkay et al. 1980) we used the observed frequency distributions of the alleles of four isoenzymes to index the differences among several populations of the blue mussel (*Mytilus edulis*) which occur along a short distance on the Atlantic Coast of Canada. It appeared that there were significant differences in genetic constitution

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which might be attributed to population differentiation among areas subjected to a restricted gene flow. However, in common with earlier workers (Koehn et al. 1976), we found that the degree of difference was not very strongly related to spatial separation and that microhabitat selection appeared as a strong possible explanation of the observed allele frequencies.

This hypothesis can be tested further if local populations in close geographic proximity but exposed to different environmental conditions are examined. The planktonic dispersal of mussel larvae must ensure that substantial gene flow occurs between populations. Mussels taken from different microhabitats within a single embayment therefore provide such a system. Studies have demonstrated that microgeographic genetic variation exists in the tidal zone (Koehn et al. 1973) and in estuaries as a clinal variation at the LAP 1 locus (Koehn et al. 1976; Lassen and Turano 1978). Furthermore, Koehn et al. (1980) has shown that there is an annual immigration of oceanic larvae into cline populations of Long Island Sound and, that there is a genotype-dependent mortality of immigrants which allows the maintenance of the LAP 1 clinal variation among adult populations.

Here we report a study of six populations from St. Margaret's Bay in Nova Scotia, Canada, surveyed for the four gene loci described earlier (Gartner-Kepkay et al. 1980) as well as one other polymorphic locus, aminopeptidase (AP). The results strongly indicate that selective pressures at the enzyme loci outweigh gene flow in the determination of the genetic makeup of local populations.

Materials and Methods

Samples of between 200 and 250 adult mussels between 30 and 50 mm total shell length were collected from each of six locations in St. Margaret's Bay, N.S. (Fig. 1). One of the populations (LI) had been sampled in the earlier study. Three of these localities were chosen at the head of the bay where there are significant tidal flats and where there is a marked influence of freshwater in the surface layers. In winter, these areas are often ice-covered. Mussels were collected from rocky formations below low water level. The three other localities may be described as subtidal but open-water sites. Two are just below low water mark on the shores of small islands and the third is off an exposed rocky shore, all near the mouth of the bay. The surface water in these latter areas is less affected by freshwater runoff. All three are typically coastal environments with salinities generally near 30‰ and with active circulation and wave action, rarely ice-covered in winter (El Din et al. 1970).

Although the six collection sites are spread over a distance of some 27 km and constitute somewhat different microhabitats, there is a strong wind-driven circulation of the water in the bay. It is essentially two-layered in summer, showing a generally estuarial vertical circulation with outflow at the surface and compensatory inflow along the bottom, within a generally counterclockwise horizontal circulation pattern. Additionally, periodically throughout the year as a result of vigorous storms, the entire water mass of the bay appears to be exchanged with waters on the coastal shelf (Platt et al. 1972). It seems highly unlikely that mollusks with pelagic larval stages could develop isolated subpopulations within such a system. For purposes of this study, it is safe to assume a virtually free exchange of larval forms throughout the bay.

One hundred animals between 30 and 40 mm in length were selected from each sample for the electrophoretic analysis. The mussel flesh was excised, homogenized, centrifuged, and the supernatant frozen following the procedure used by Gartner-Kepkay et al. (1980). Horizontal starch gel electrophoresis using the discontinuous Poulik buffer system of Singh and Zouros (1978) was employed. This technique of separating isoenzymes electrophoretically permits the detection of allelic variants at individual gene loci and the inference of mendelian variation in populations (Levinton and Koehn 1976). The genetic variability at five gene loci was determined simultaneously. The isoenzymes recorded were leucine aminopeptidase 1 (LAP 1), peptidase 2 (PEP 2; formerly termed LAP 2), phosphoglucose isomerase (PGI), phosphoglucose mutase (PGM), and aminopeptidase (AP). The staining techniques used were those of Shaal and Anderson (1974) and Shaw and Prasaad (1970) with minor modifications.

Results

The five loci (LAP 1, PEP 2, PGI, PGM, and AP) were all polymorphic and alleles were designated according to their relative electrophoretic mobility.

LAP 1

Three alleles common to all localities were identified, i.e. LAP 1^{98}, LAP 1^{96}, and LAP 1^{94}. The frequency of LAP 1^{98} ranges from 0.37 in LI and SII to 0.63 in FP. LAP 1^{94} ranges from 0.30 in LI to 0.06 in PI (Table 1). As can be seen in Fig. 2a, the six localities appear to fall into two groups. SII, LI, and NWC appear to comprise a group where alleles are distributed uniformly. This is in contrast with a second group composed of PI, TI, and FP where LAP 1^{98} is the predominant allele. Paired comparisons of allele frequency distributions using the chi-square test for heterogeneity indicate that the differences between groups are significant whereas within-group comparisons are not (Table 2).

PEP 2

Four alleles common to all localities were present, i.e. PEP 2^{110}, PEP 2^{100}, PEP 2^{95}, PEP 2^{90}. PEP 2^{100} ranges from 0.15 in LI to 0.45 in FP, whereas PEP 2^{90} ranges from 0.12 in TI to 0.45 in LI (Table 1). Figure 2b shows that the localities LI, SII, and NWC have predominantly slow migrating alleles (PEP $2^{90\&95}$), whereas PI, TI, and FP have a predominance of the faster migrating allele (PEP 2^{100}). Chi-square values for paired comparisons (Table 2) are significant except for the pairs NWC–LI, PI–FP, and PI–TI.

PGM

Five alleles were common to all localities, i.e. PGM^{110}, PGM^{100}, PGM^{95}, PGM^{90}, and PGM^{85}. A rare sixth allele

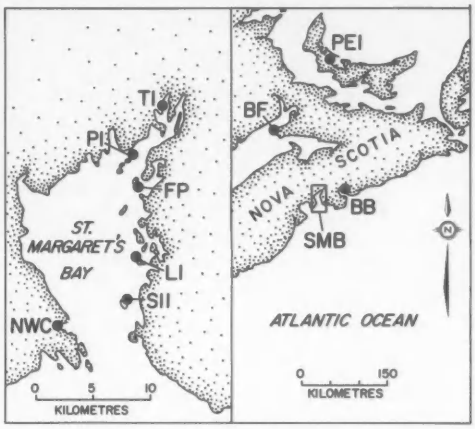

FIG. 1. Mussel sampling locations: Prince Edward Island (PEI), Bay of Fundy (BF), Bedford Basin (BB), St. Margaret's Bay (SMB), Todd's Island (TI), Potato Island (PI), Frenchman's Point (FP), Luke Island (LI), Shut-In Island (SII), North West Cove (NWC). LI was the sampling site of our SMB population in Gartner-Kepkay et al. 1980.

PGM^{80} occurred in low frequencies in all localities except for TI where it was absent. PGM^{90} ranges from 0.17 in PI to 0.34 in LI, and PGM^{100} ranges from 0.15 in LI to 0.37 in PI (Table 1). Figure 2c shows that the slow migrating allele (PGM^{90}) again predominates in the "open-water" sites whereas "head-water" localities have the faster migrating alleles (PGM^{95} and PGM^{100}) predominating. The data in Table 2 indicate that the paired comparisons within groups are not significantly different. All other chi-square values are significant with the exception of that for the SII−TI pair.

PGI

Four alleles were common to all localities, i.e. PGI^{100}, PGI^{97}, PGI^{92}, and PGI^{90}. All alleles show substantial frequency ranges and there is no obvious grouping of localities with respect to allele frequency distributions (Table 1). However, in Fig. 2d it does appear that at least LI and NWC have predominantly slow migrating alleles whereas TI and FP have predominantly faster migrating alleles. Paired comparisons show that all localities are significantly different from each other except the pairs SII−FP, PI−FP, and FP−TI (Table 2).

AP

Four alleles were common to all localities, i.e. AP^4, AP^3, AP^2, AP^1. Allele frequency ranges are not extensive among localities (Table 1) and, as shown in Fig. 2e, the six localities have similar frequency distributions where AP^3 is the dominant allele. The only exception is NWC where AP^2 is dominant. Table 2 indicates that NWC is significantly different from the other five localities. All other paired comparisons show chi-square values to be not significant except for the pair PI−FP.

TABLE 1. The allele frequencies for each locus observed in six locations in St. Margaret's Bay.

Locality	Allele					
	LAP 1	98	96	94		
NWC		0.43	0.37	0.20		
SII		0.37	0.41	0.22		
LI		0.37	0.33	0.30		
PI		0.61	0.34	0.06		
FP		0.63	0.27	0.10		
TI		0.60	0.32	0.08		
	PEP 2	110	100	95	90	
NWC		0.03	0.17	0.42	0.39	
SII		0.08	0.30	0.38	0.25	
LI		0.03	0.15	0.39	0.45	
PI		0.13	0.38	0.33	0.16	
FP		0.07	0.45	0.35	0.14	
TI		0.21	0.33	0.34	0.12	
	PGM	110	100	95	90	85	80
NWC		0.08	0.19	0.30	0.31	0.10	0.03
SII		0.09	0.21	0.29	0.33	0.07	0.01
LI		0.07	0.15	0.29	0.34	0.12	0.05
PI		0.08	0.37	0.36	0.17	0.02	0.02
FP		0.05	0.33	0.35	0.24	0.04	0.01
TI		0.06	0.29	0.35	0.26	0.04	0.00
	PGI	100	97	92	90		
NWC		0.08	0.20	0.58	0.15		
SII		0.10	0.31	0.33	0.26		
LI		0.07	0.17	0.47	0.29		
PI		0.14	0.29	0.45	0.13		
FP		0.12	0.38	0.34	0.17		
TI		0.18	0.41	0.24	0.17		
	AP	4	3	2	1		
NWC		0.07	0.38	0.43	0.13		
SII		0.13	0.42	0.30	0.16		
LI		0.16	0.36	0.33	0.16		
PI		0.09	0.43	0.30	0.19		
FP		0.19	0.36	0.26	0.20		
TI		0.13	0.41	0.29	0.18		

Nei's (1972) index of genetic identity was used to show the degree of similarity among pairs of localities. Table 3 shows a matrix of genetic identity values for each locus. In two of the loci, LAP 1 and PGM, the "open-water" sites (NWC, SII, and LI) and the "head-water" sites (PI, TI, and FP) show consistently higher within-group values than values calculated between groups. This trend becomes less obvious in PEP 2 and is least apparent in PGI and AP. PGI exhibits the greatest range of identity values from 0.677 to 0.983 indicating a greater degree of dissimilarity among localities. AP, on the other hand, shows identities to be high and displays the smallest range of identity values suggesting that localities are very similar.

To show whether the grouping of localities could be justified, the 15 identity values were separated into two groups, within-group comparisons (six values) and between-group comparisons (nine values). This was done for each locus separately. The two sets of values were compared using the Wilcoxon Two-Sample Rank Test (Sokal and Rohlf 1969).

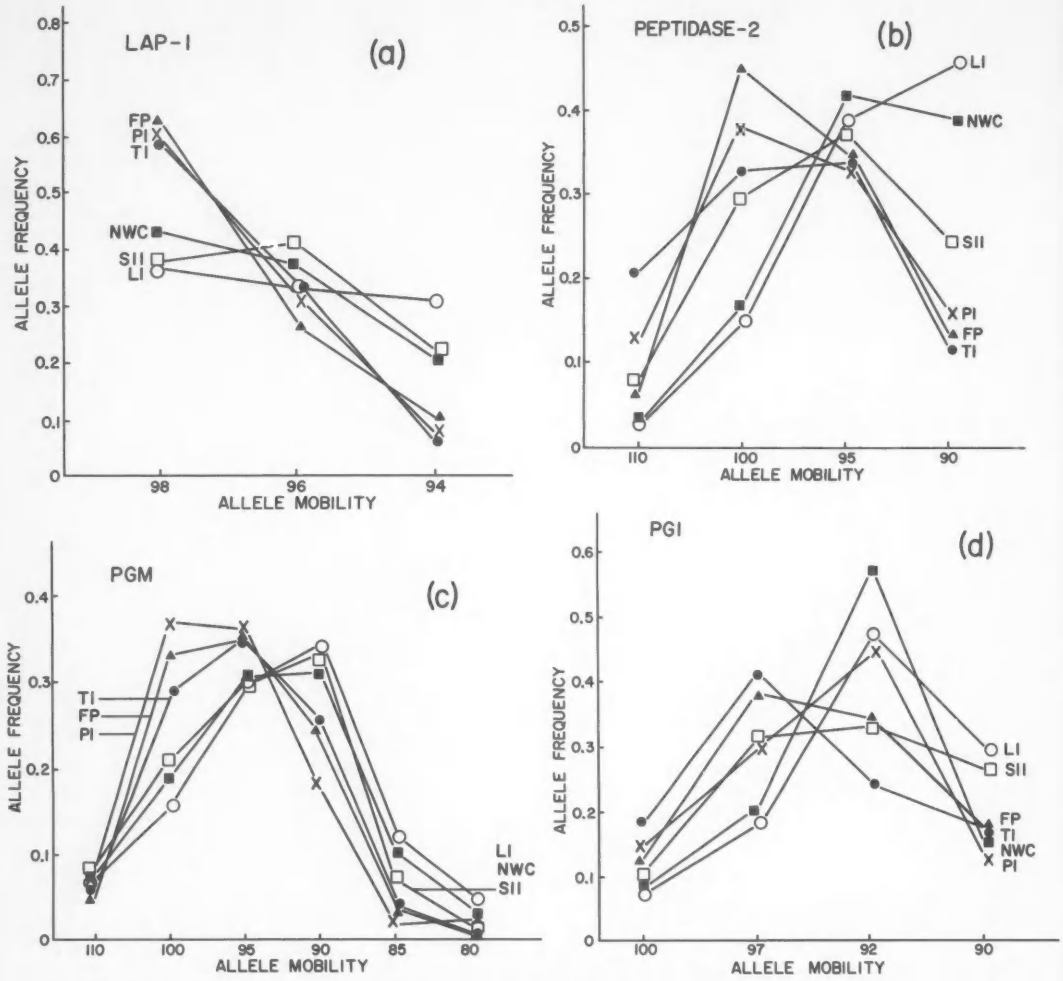

FIG. 2. Graphical representation of allele frequency distribution for each locality. The x-axis is dimensionless and represents the assigned relative mobility values detected at each locus. Fig. 2a shows the allele frequencies of LAP I for all six localities. Fig. 2b shows the allele frequencies of PEPTIDASE-2 for all six localities. Fig. 2c shows the allele frequencies of PGM for all six localities. Fig. 2d shows the allele frequencies of PGI for all six localities. Fig. 2e shows the allele frequencies of AP for all six localities.

PGM, LAP 1, and PEP 2 all displayed within-group identities that are significantly higher than between-group values. This was not the case for PGI and AP. However, when the same test was performed on mean genetic identity values (Table 3), the trend for higher identities for the within-group comparisons was confirmed.

The foregoing analysis shows that populations at the head of the embayment are genetically different from those at the mouth of the embayment. Even in the light of gene flow which must occur among populations occupying this same inlet, the observation of this differentiation alone does not provide evidence for selection because differentiation can be accidental (for example, through genetic drift or through the bottleneck or founder effects), and genetic similarity among "head-water" or "open-water" populations may be explained as a result of geographic proximity of localities within each group. The following analysis will provide evidence that the differentiation is most likely the result of natural selection.

In our previous study (Gartner-Kepkay et al. 1980), two geographically distant populations of the blue mussel exposed to little environmental variation (Fig. 1; BB and SMB) were found to be more similar to each other than they were to either

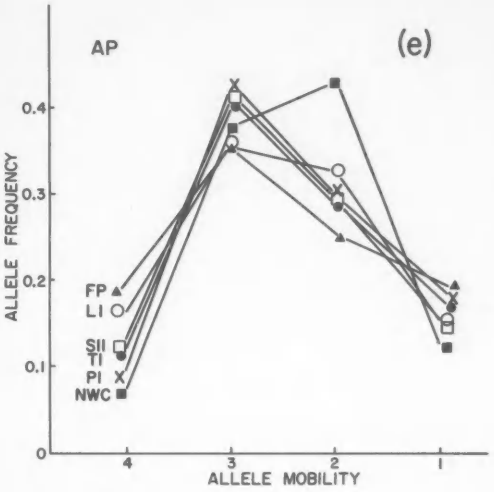

FIG. 2. (*Concluded.*)

of two populations occupying widely fluctuating environments (BF and PEI). The latter two populations were more similar to each other than to either BB or SMB. In Table 4 the mean allele frequencies for the BF−PEI group (group I) and the BB−SMB group (group II) are given. Mean frequencies are also calculated for the TI−PI−FP group (group III) and the LI−SII−NWC group (group IV). The mean allele frequency was calculated for all loci except for AP which was not assayed in our previous study. Also, the "92" allele of PGI was pooled with the "90" allele. The "92" allele was discovered in our present study and represents a new mobility very close to mobility "90." It is very likely that in our earlier study we had inadvertently pooled the two alleles into one class designated as "90." Shown in Table 4 are the values of D_A and D_B, where D_A is defined as the difference in mean allele frequency between group I and group II (D_A = I − II) and D_B is the difference in mean allele frequency between group III and group IV (D_B = III − IV). The point of interest to note is the concordance or discordance with the signs of D_A and D_B. It can be seen from the table that there are 14 concordances and 2 discordances. For each locus there are $n-1$ degrees of freedom for the sign of allele frequency differences (where n is the number of alleles). Conservatively, we may accept 2 discordances out of 12 independent cases. If concordances and discordances are equally probable, then the probability of the observed event is 0.0193. From this analysis we can conclude that, as one moves from populations experiencing wide environmental fluctuations (groups I and III) to populations of more stable environments (groups II and IV), the gene frequencies change in the same direction regardless of whether the populations are distantly or proximally spaced.

Further evidence for selection comes from the clustering of the 10 populations (the 4 in our first study and the 6 in our present study) according to their genetic identities. These identity values are based on the four loci studied in all 10 populations (Fig. 1), and are shown in Table 5. A

TABLE 2. Probability levels of paired comparisons of allele distributions using chi-square tests. (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns = not significant.)

LAP 1	NWC	SII	LI	PI	FP	TI
NWC						
SII	ns					
LI	ns	ns				
PI	***	***	***			
FP	***	***	***	ns		
TI	***	***	***	ns	ns	
PEP 2	**NWC**	**SII**	**LI**	**PI**	**FP**	**TI**
NWC						
SII	***					
LI	ns	***				
PI	***	*	***			
FP	***	*	***	ns		
TI	***	***	***	ns	***	
PGM	**NWC**	**SII**	**LI**	**PI**	**FP**	**TI**
NWC						
SII	ns					
LI	ns	ns				
PI	***	***	***			
FP	***	*	***	ns		
TI	*	ns	***	ns	ns	
PGI	**NWC**	**SII**	**LI**	**PI**	**FP**	**TI**
NWC						
SII	***					
LI	***	***				
PI	*	**	***			
FP	***	ns	***	ns		
TI	***	**	***	***	ns	
AP	**NWC**	**SII**	**LI**	**PI**	**FP**	**TI**
NWC						
SII	*					
LI	*	ns				
PI	*	ns	ns			
FP	***	ns	ns	*		
TI	*	ns	ns	ns	ns	

"dendrogram" (Fig. 3) was thus produced according to standard techniques (Sokal and Sneath 1963). The "dendrogram" shows populations falling into three distinct groups:

1) NWC−LI−SII−SMB−BB group (stable environments).
2) PI−TI−FP−BF group (fluctuating environments).
3) PEI group (fluctuating environment).

Within each group genetic identities are high and have small variances (the mean identities and their standard errors are 0.947 ± 0.009 for the first group and 0.966 ± 0.008 for the second group). The mean identity for between-group comparisons is 0.877 ± 0.011. The PEI population does not cluster with either group, but is closer to the second group (mean identity = 0.881) than to the first (mean identity = 0.739). This, again, is consistent with the fact that PEI is a widely fluctuating environment. This type of clustering is not expected on the basis of geographic proximity and provides further evidence that environmental factors are

TABLE 3. Genetic identity values between pairs of localities for each locus and for the mean of loci.

LAP 1	NWC	SII	LI	PI	FP	TI
NWC		0.994	0.977	0.948	0.935	0.951
SII			0.983	0.909	0.888	0.912
LI				0.877	0.876	0.887
PI					0.994	0.999
FP						0.996
TI						
PEP 2	NWC	SII	LI	PI	FP	TI
NWC		0.945	0.994	0.831	0.791	0.676
SII			0.911	0.969	0.948	0.802
LI				0.784	0.739	0.632
PI					0.991	0.838
FP						0.810
TI						
PGM	NWC	SII	LI	PI	FP	TI
NWC		0.995	0.992	0.888	0.943	0.965
SII			0.984	0.898	0.948	0.969
LI				0.835	0.902	0.927
PI					0.987	0.973
FP						0.996
TI						
PGI	NWC	SII	LI	PI	FP	TI
NWC		0.677	0.957	0.959	0.875	0.761
SII			0.942	0.950	0.983	0.946
LI				0.931	0.884	0.782
PI					0.965	0.898
FP						0.979
TI						
AP	NWC	SII	LI	PI	FP	TI
NWC		0.842	0.847	0.839	0.809	0.837
SII			0.993	0.997	0.986	1.000
LI				0.984	0.985	0.990
PI					0.976	0.996
FP						0.990
TI						
Mean identity	NWC	SII	LI	PI	FP	TI
NWC		0.891	0.953	0.893	0.871	0.838
SII			0.963	0.945	0.951	0.923
LI				0.882	0.877	0.844
PI					0.983	0.941
FP						0.954
TI						

the main causes of genetic differentiation of populations on either a micro- or macro-geographical scale.

Hardy–Weinberg equilibrium tests for each locus and each locality indicate that for LAP 1, PEP 2, PGM, and PGI, the observed zygotic distributions for all localities do not conform to what is expected under equilibrium. In all these cases, there is a significant deficiency in the number of heterozygotes. The sole exception is locus AP at localities NWC, PI, and FP. The deficiency in the number of heterozygotes was measured by

$$D = \frac{H_{ob} - H_{ex}}{H_{ex}}$$

where H_{ob} is the observed number of heterozygotes, and H_{ex} is the expected number of heterozygotes under Hardy–Weinberg equilibrium. The D values are given in Table 6 and are tested for homogeneity. D values among loci are always significantly different, whereas values tested among localities may or may not be significant. If the deficiency of heterozygosity resulted from population subdivision (Wahlund Effect), one might expect a more uniform distribution of the D values within each locality. A constancy of locus-specific D values is more compatible with selection acting against heterozygotes at some time in the animal's life cycle. The locus-specific selection pressure must vary little among localities, but it must vary considerably from locus to locus. The evidence for selection against the heterozygote is, nonetheless, only indirect, and the whole problem of heterozygote deficiency remains basically unresolved (Zouros et al. 1980).

Discussion

It is clear that the five gene loci show a sequence in the degree of variation both within and between sampling localities. The LAP 1 locus clearly divides the six localities into two groups of three, corresponding closely with our a priori classification into "head-water" and "open-water" sites. The two groups are also apparent among the PEP 2 and PGM loci. By contrast, the PGI locus shows high overall variability although the location pattern is missing, whereas the AP locus shows rather uniform distribution among samples with reduced overall heterogeneity.

The geographic grouping signaled by the LAP 1 locus is consistent with Koehn et al. (1976) interpretation of this gene locus as having a function related to salinity tolerance. A very similar grouping of collection sites showed up in our previous study of different populations, and was similarly attributed. Subsequent to that study (Gartner-Kepkay et al. 1980), Dr Richard Koehn (personal communication) has kindly provided data for LAP-1 on additional mussel populations around the Atlantic Maritimes. His populations of northern Cape Breton and Gulf of St. Lawrence closely resemble our neighboring PEI population, whereas his two Maine populations are like our Apple River and Digby Neck (unpublished data) populations of the Bay of Fundy which is part of the same water system. In both cases, populations are described by the dominance of the fast migrating allele LAP-1^{98}. His Atlantic Coast populations, while not identical with our populations from the same general area, display a similar trend in that the faster migrating allele of LAP 1 becomes less dominant than in the populations from Cape Breton to PEI or Bay of Fundy regions. An almost identical set of locality classes emerges from the PEP 2 and PGM loci both within St. Margaret's Bay and between sites in our previous study, strongly suggesting that these loci are subject to much the same or closely associated environmental selection factors as affect LAP 1.

On this hypothesis, the lack of patterning among sample localities on the basis of the PGI and AP loci is revealing, particularly in association with the results of the test for departure from Hardy–Weinberg equilibrium. All the four isoenzymes that we examined earlier showed, for all populations, departures from equilibrium which were statistically significant at probability levels of less than 0.001. The same

TABLE 4. Comparison of mean allele frequencies of mussels from various sites in the Atlantic Maritimes.[a] See Fig. 1 for specific locations.

	Macrogeographical study (Gartner-Kepkay et al. 1980) group I: PEI, BF group II: BB, SMB			Microgeographical study (present study) group III: TI, PI, FP group IV: LI, SII, NWC		
	Mean frequencies			Mean frequencies		
	Group I	Group II	D_A (I−II)	Group III	Group IV	D_B (III−IV)
LAP 1^{98}	0.555	0.420	0.135	0.613	0.390	0.223
LAP 1^{96}	0.345	0.310	0.035	0.310	0.370	−0.060[b]
LAP 1^{94}	0.100	0.245	−0.145	0.080	0.240	−0.160
PEP 2^{110}	0.410	0.115	0.295	0.137	0.047	0.090
PEP 2^{100}	0.390	0.250	0.140	0.387	0.207	0.180
PEP 2^{95}	0.225	0.270	−0.045	0.340	0.397	−0.057
PEP 2^{90}	0.075	0.365	−0.290	0.140	0.363	−0.223
PGI^{100}	0.375	0.120	0.225	0.220	0.083	0.137
PGI^{97}	0.315	0.235	0.080	0.360	0.227	0.133
$PGI^{90\&92}$	0.315	0.645	−0.330	0.250	0.346	−0.096
PGM^{110}	0.150	0.080	0.070	0.063	0.080	−0.017[b]
PGM^{100}	0.340	0.220	0.120	0.330	0.183	0.147
PGM^{95}	0.275	0.215	0.060	0.353	0.293	0.060
PGM^{90}	0.205	0.360	−0.155	0.223	0.327	−0.104
PGM^{85}	0.030	0.090	−0.060	0.033	0.097	−0.064
PGM^{80}	0.000	0.035	−0.035	0.010	0.030	−0.020

[a]Test for equiprobable sign:

$$P = \Pr(0) + \Pr(1) + \Pr(2) = (0.5)^{16} + 16(0.5)^{16} + \frac{16 \times 15}{2}(0.5)^{16}$$

$P = 0.002$.

But one sign is constrained in each locus; a conservative test will be two discordances out of 12 cases:

$$P = (0.5)^{12} + 12(0.5)^{12} + \frac{12 \times 11}{2}(0.5)^{12} = 0.0193 = 0.02.$$

[b]Two discordances in sign of D out of 16 cases.

TABLE 5. Genetic identities among 10 mussel populations. The groupings are those produced by the cluster analysis shown in Fig. 3.

	BF	TI	FP	PI	BB	SMB	SII	LI	NWC	PEI
BF	—	0.966	0.926	0.936	0.882	0.835	0.893	0.733	0.824	0.951
TI		—	0.945	0.927	0.910	0.897	0.904	0.807	0.838	0.890
FP			—	0.984	0.913	0.905	0.942	0.850	0.886	0.847
PI				—	0.916	0.907	0.931	0.857	0.906	0.836
BB					—	0.988	0.966	0.965	0.969	0.804
SMB						—	0.971	0.982	0.978	0.753
SII							—	0.955	0.903	0.774
LI								—	0.980	0.657
NWC									—	0.708
PEI										—

is true for all the microhabitats tested here. Furthermore, all show strong heterozygote deficiencies. However, the situation for the AP locus is quite different; three of the sampled sites showed no significant departure from Hardy−Weinberg equilibrium and even for those that show departure, the calculated heterozygote deficiency is lower than are values for other gene loci.

The AP results suggest the hypothesis that individuals examined from all the various sampling localities within St. Margaret's Bay had come from a more or less homogeneous spawning stock. Selective action by environmental factors appears to have very little influence on this locus, suggesting that its function is related to some fundamental property of the species, *M. edulis*. If this is so, however, the different patterns emerging among the other four loci are suggestive of possible selection against heterozygotes resulting in different genic proportions in the stocks settling and surviving in different localities.

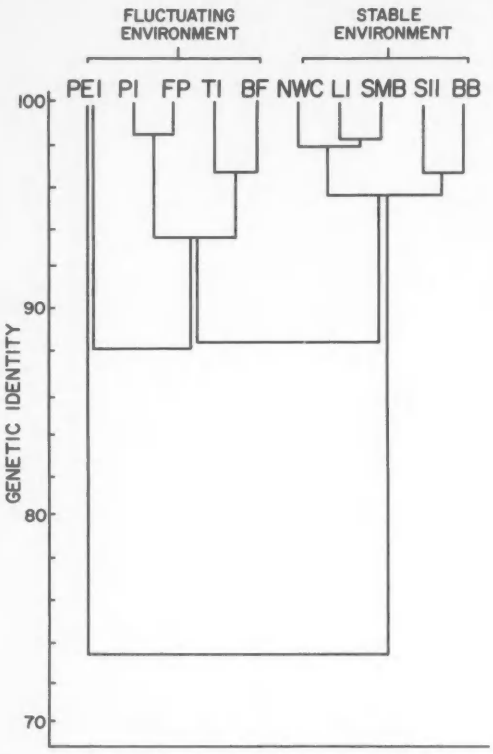

FIG. 3. A clustering of 10 mussel populations according to genetic identity.

TABLE 6. Heterozygote deficiency values for all localities and all loci. Probability levels resulting from tests for homogeneity among loci and localities are shown in the row and column margins, respectively.

	LAP 1	PEP 2	PGM	PGI	AP	
NWC	−0.311	−0.668	−0.334	−0.577	−0.103	***
SII	−0.567	−0.526	−0.396	−0.331	−0.227	*
LI	−0.518	−0.457	−0.435	−0.350	−0.124	*
PI	−0.716	−0.304	−0.485	−0.297	−0.001	***
FP	−0.596	−0.404	−0.438	−0.302	−0.089	***
TI	−0.680	−0.568	−0.431	−0.470	−0.165	***
	**	*	ns	ns	ns	

The strong parallels of our present findings with our earlier comparison among embayments suggest that environmental selection is the most likely explanation for the genetic differences apparent among populations facing extensive gene flow. In comparing our six populations with our previous four (a situation of restricted gene flow), we showed that the localities cluster according to environment and not geographical proximity (Fig. 3). Allele frequencies, particularly those of LAP 1, PEP 2, and PGM, appear to offer a strong index of environmental conditions where a clear shift towards the more mobile alleles indicates situations liable to terrestrial runoff, relatively severe winters, and generally more variable ambient conditions. In the case of PGI, selection pressures are not well indexed by our classification of environments by locality. However, when the mean allele frequencies of groups are compared (Table 4), it appears that the distribution of PGI alleles is not totally independent of the other three loci in that the allele frequencies change in the same general direction as one moves from "open-water" environments to "head-water" environments.

These findings suggest that in the case of *M. edulis* it may be that the species has, over time, developed a large capacity for genoadaption to the highly variable environment which must be withstood by the relatively sessile adults. Although we still know very little about the function of the isoenzymes that we have found to be polymorphic, it appears that certain of them are highly sensitive to changing habitat conditions and might therefore constitute indices of these changes when used in association with other gene population components not similarly affected. Our own interest extends particularly to an interest in the extent to which such suites of enzymes might be used to index production parameters of various subpopulations.

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Winter Distribution of Juvenile Coho Salmon (*Oncorhynchus kisutch*) Before and After Logging in Carnation Creek, British Columbia, and Some Implications for Overwinter Survival

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TSCHAPLINSKI, P. J., AND G. F. HARTMAN. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40: 452 – 461.

Numbers of juvenile coho salmon (*Oncorhynchus kisutch*) in streams are reduced substantially in winter compared to those that occur in summer. Most of this reduction occurs early in autumn with the onset of the first seasonal freshets. Stream sections containing adequate winter habitat in the form of deep pools, log jams, and undercut banks with tree roots and debris lost fewer fish during freshets and maintained higher numbers of coho in winter than sections without these habitat characteristics. These features provide shelter and reduce stream velocities. Microhabitats occupied by coho juveniles in winter after logging were unchanged from those described before logging — all microhabitats were characterized by low water velocities (≤0.3 m/s). Up to 48% of the coho population inhabiting stream sections with adequate shelter remained there by midwinter (Jan. 3). This percentage was typical of stream sections where at least some trees remained after logging. Streamside trees stabilized the banks and prevented their collapse. In contrast, two of three study sections that had been clear-cut logged had unstable banks which collapsed during winter freshets. Almost no coho remained in these sections in winter. Many coho emigrate from the main stream to seek the shelter of low-velocity tributaries and valley sloughs concurrent with the decline of coho populations in Carnation Creek during autumn and early winter. This seasonal shift in distribution reverses in the spring when large numbers of coho reenter the main stream. Fish overwintering in these sites have a high apparent survival rate. Before logging a 4-yr mean of 169 ± 44 coho entered one tributary (a slough called 750-m site) in autumn. Of these numbers entering, 72.2% came out in spring. During and after logging, an annual mean of 288 coho entered the same site. The apparent survival rate during and after logging was 67.4%, essentially unchanged from the prelogging value. Logging has neither reduced the numbers of coho juveniles that enter such sites in autumn to overwinter, nor reduced the numbers leaving these sites to reenter Carnation Creek in spring.

TSCHAPLINSKI, P. J., AND G. F. HARTMAN. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40: 452 – 461.

Le nombre de jeunes saumons coho (*Oncorhynchus kisutch*) dans le cours d'eau diminue substantiellement en hiver comparativement à ce qui se produit en été. Cette diminution survient surtout à l'automne, avec le début des premières crues saisonnières. Les sections du cours d'eau contenant des habitats hivernaux adéquats, tels que fosses profondes, embâcles de buches et berges sapées avec racines d'arbres et débris, perdent moins de poissons durant les crues et maintiennent plus de saumons coho en hiver que les sections dépourvues de ces caractéristiques d'habitat. Ces dernières fournissent des abris et ralentissent les courants. Les microhabitats occupés par les saumoneaux en hiver après exploitation forestière ne diffèrent pas de ceux décrits avant l'exploitation — tous les microhabitats sont caractérisés par de faibles vitesses de courants (≤ 0,3 m/s). Jusqu'à 48 % de la population de saumons coho habitant les secteurs munis d'abris adéquats y sont encore à la mi-hiver (3 janvier). Ce pourcentage est typique des secteurs du cours d'eau où au moins quelques arbres sont encore présents après l'exploitation forestière. Les arbres stabilisent les berges et empêchent leur

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affaissement. Par contre, deux des trois secteurs étudiés qui avaient été coupés à blanc avaient des berges instables qui se sont affaissées lors des crues hivernales. À cette saison, très peu de saumons y demeurent. Plusieurs sujets émigrent hors du cours d'eau principal et cherchent un abri dans les tributaires à courant moins rapide et munis de dépressions, en même temps que se produit un déclin des populations de saumons coho dans le ruisseau Carnation en automne et au début de l'hiver. Ce glissement saisonnier de la distribution s'inverse au printemps alors qu'un grand nombre de sujets pénètrent de nouveau dans le cours d'eau principal. Le taux de survie apparent des poissons hivernant à ces endroits est élevé. Avant l'exploitation forestière, une moyenne de 169 ± 44 saumons pénétrèrent dans un tributaire (une fondrière dénommée site 750 m) en automne. Sur ces nombres, 72,2 % en sortirent au printemps. Pendant et après l'exploitation forestière, une moyenne annuelle de 288 saumons pénétrèrent dans le même site. Le taux de survie apparent pendant et après l'exploitation a été de 67,4 %, essentiellement le même qu'avant l'exploitation. Cette dernière n'a donc pas réduit le nombre de juvéniles pénétrant à ces endroits en automne afin d'y hiverner, non plus que réduit le nombre qui en sortent pour pénétrer de nouveau dans le ruisseau Carnation au printemps.

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JUVENILE coho salmon (*Oncorhynchus kisutch*) occupy a wide variety of stream habitats in summer. Areas occupied include pools (with or without bank cover), slow-moving riffles and side channels, midstream locations, locations under or near banks, and areas jammed with logs and other large debris (Hartman 1965; Ruggles 1966). Several investigators have documented that stream-dwelling coho undergo seasonal shifts in distribution (Bustard and Narver 1975a, b; Mason 1976). Spatial requirements in winter differ from those in summer (Mason 1976). Mason (1966) reported that during winter when water temperatures were low (5–8°C in Oregon), coho fry aggregated near the bottoms of pools in the main stream, remained close to each other, and were quiescent. Bustard and Narver (1975a) demonstrated that young coho in autumn move into deep, slow-moving water as stream temperatures decline and discharge volumes increase. These investigators concluded that coho in winter must avoid (a) downstream displacement and physical injury during freshets (floods), and (b) predation by birds and mammals. They determined that important overwintering sites are (1) under banks, along stream margins where water movement is slow (≤0.15 m/s), (2) flooded sloughs in the stream valley that contain rooted vegetation, and (3) low-velocity side channels and small tributaries that sometimes contain flowing water only in winter. Coho also seek the shelter provided by large masses of debris (e.g. tree roots and logs) as seasonal water temperatures fall (Bustard and Narver 1975a).

Logging may affect the overwinter survival of coho in several ways. For example, Toews and Moore (1982) have shown that logging operations along stream sections in which (1) all trees are removed to the banks, and (2) felled trees are removed from the stream, eventually result in less debris accumulating in the stream and also cause debris masses to be less stable compared to stream sections not subjected to such logging practices. Winter freshets may thus remove debris cover and erode banks more readily in such logged areas than in unlogged locations.

Because banks and debris cover provide overwintering habitats important to juvenile coho (Bustard and Narver 1975a), and because some logging practices may eliminate or alter this cover (Toews and Moore 1982), logging can potentially reduce populations of stream-dwelling coho in winter. Therefore, one major objective of this research was to describe the numbers and distribution of coho juveniles overwintering in selected sections of a British Columbia coastal stream in relation to (1) the distribution of freshets, and (2) different logging practices applied in each stream section.

Bustard and Narver (1975a) demonstrated that large numbers of juvenile coho salmon leave the main stream in autumn to enter side channels, sloughs, and tributaries to overwinter. The same coho then reenter the main stream in spring. Bustard and Narver (1975a) reported that coho that moved into these sheltered habitats in autumn survived the winter at twice the rate as those which remained in the main stream. The second objective of this paper was to compare the numbers of coho entering sloughs and tributaries in autumn with numbers reentering the main stream in spring for several years both before and during logging.

Study Area

Carnation Creek is a small stream, about 7.8 km long, flowing into Barkley Sound on the west coast of Vancouver Island. The stream drains an area ~10 km^2 in the "Coastal Western Hemlock Biogeoclimatic Zone" of British Columbia (Hartman et al. 1982). Annual precipitation varies from 250 to 380 cm, most of which falls between early September and late March. Discharge volumes fluctuate rapidly and widely during winter from about 0.2 m^3/s up to 46 m^3/s during frequent winter freshets. The area, stream, and fish populations are described by Hartman et al. (1982).

Two areas in the Carnation Creek valley inhabited by many coho fry ["age 0" fish, Bustard and Narver (1975a, b)] and yearlings ["age 1+" fish, Bustard and Narver (1975a, b)] are a slough (called "750-m site") located 750 m upstream from the mean summer high-tide mark, and a low-velocity tributary at 1600 m (called 1600 Tributary). These sites are as described by Bustard and Narver (1975a) except that clear-cut logging has since removed all trees from both areas and left

TABLE 1. Data for the Carnation Creek study sections used to enumerate overwintering coho. Two values for area and volume (plus seasonal mean values in parentheses) are given for "cover" in section VI due to the midwinter addition of new cover when a large root mass fell into the stream.

Study section	Length (m)	Cover available for coho: Area (m^2)	Cover available for coho: Debris vol (m^3)	Logging method used: Streamside strip of trees (% of bank covered)	Logging method used: Log hauling across the stream
B (at "B-weir")	38	26.0	46.0	100	None
III	62	41.0	37.0	80	None
VI	77	5.0–8.0 (6.5)	2.5–5.0 (3.8)	0	Yes (limited)
VIa	8	2.5	3.0	0	None
VII	27	2.0	2.0	0	None

debris in 1600 Tributary. The 750-m site consists of seasonally flooded channels (usually filled with water during autumn, winter, and spring) that meander through areas thick with rooted vegetation (sedges and grasses). Both sites also contain small shrubs that provide cover over the flooded channels (see Bustard and Narver 1975a).

Materials and Methods

Enumeration of Populations Overwintering in Carnation Creek

Visual counts of coho fry and yearlings overwintering in five selected sections in the Carnation Creek main channel were made from October 3, 1980 to March 20, 1981. The lengths of the study sections, the amount of cover available to overwintering coho, and the logging practices conducted at each site are summarized in Table 1. Cover was defined to comprise (a) the area of bank that overhung the stream, in addition to (b) the area of woody debris that occurred in the stream. Both types of cover were measured in the field using 30-m tapes. The total volume of this cover was determined by measuring the lengths, widths, and depths of such habitat that would be available to coho juveniles during periods of high discharge volumes (i.e. ≥ 10 m^3/s).

Counts were made in stream sections that represented two different methods of logging. Section III and the site ~25 m upstream from the "B" hydrographic weir (Section B) were at least partly "forested." Logging was conducted along both sides of the stream in these sections but streamside strips of trees were left in both areas. These strips, which varied from 5 to 40 m wide, consisted of trees that either could not be felled away from the stream or could not be hauled up over the crests of steep cliffs that bordered the stream valley. No logging-related activity occurred within the stream channel, and all large, woody debris in the stream was left undisturbed. Section B contained shallow pools overhung by grassy banks at its lower end. The upstream portion was comprised entirely of a large pool with deeply undercut banks, large tree roots, and much debris in the form of jammed logs. The pool was 3 m deep in its center. Section III contained a long riffle about 20 m in length. This section had deep pools with fallen logs and tree roots at its upstream end.

Three sections, VI, VIa, and VII, were located in a large clear-cut area where all trees had been removed up to the stream banks. No overhead cover from vegetation was present. These sections were located in a part of the stream valley where logging practices included: (a) falling all trees up to the stream bank, (b) hauling some felled trees across or out of the stream, (c) dragging out from the stream commercially valuable trees that had fallen into it before logging, and (d) killing non-commercial tree species (especially red alder, *Alnus rubra*) by girdling bark from the trunks and by applying herbicide. This type of logging resulted in changes in the morphology of the stream channel. Section VI was essentially a straight channel (77 m long) which contained rapidly flowing water when the discharge volume was >0.5 m^3/s. This section contained little shelter in the form of pools or cover provided by undercut banks. Two small (often isolated) pools along the south side of the stream always contained coho juveniles. These pools contained tree roots and debris. In contrast to these sites, sections VIa (immediately upstream from VI) and VII contained large debris and large root masses located in deep pools. The pools in section VIa also contained deeply undercut banks in which fish could take refuge.

Ten visual counts of resident fry and yearlings were made in each section during the course of the study. Observations were made by snorkeling in the stream, and a handheld flashlight aided in locating fish residing under banks and in other poorly lit areas. Data were recorded by a field assistant, and all sections were enumerated on the same day. All counts were made between freshet periods when the discharge volumes ranged from 0.12 to 1.10 m^3/s. Four counts were made immediately after a major freshet to observe any resulting changes in population numbers.

Visual counts were confirmed by estimates made of the sizes of the coho populations. The Seber-LeCren (1967) removal method was used to calculate population sizes, and fish in Carnation Creek were sampled using electrofishing and pole-seine equipment. Comparison of results from visual counts with those from population estimates indicated that thorough visual enumeration using flashlights produced data that agreed with those of the alternate method. Population estimates were made in sections III and VI on September 16–17, 1980 and again on October 9, 1980. "Fry" (fish <1 yr old) and yearlings were distinguished visually. All fish ≥ 75 mm long were considered to be yearlings. Water velocity measurements were taken in March with a Gurley "Pygmy" current meter in areas where fish had overwintered.

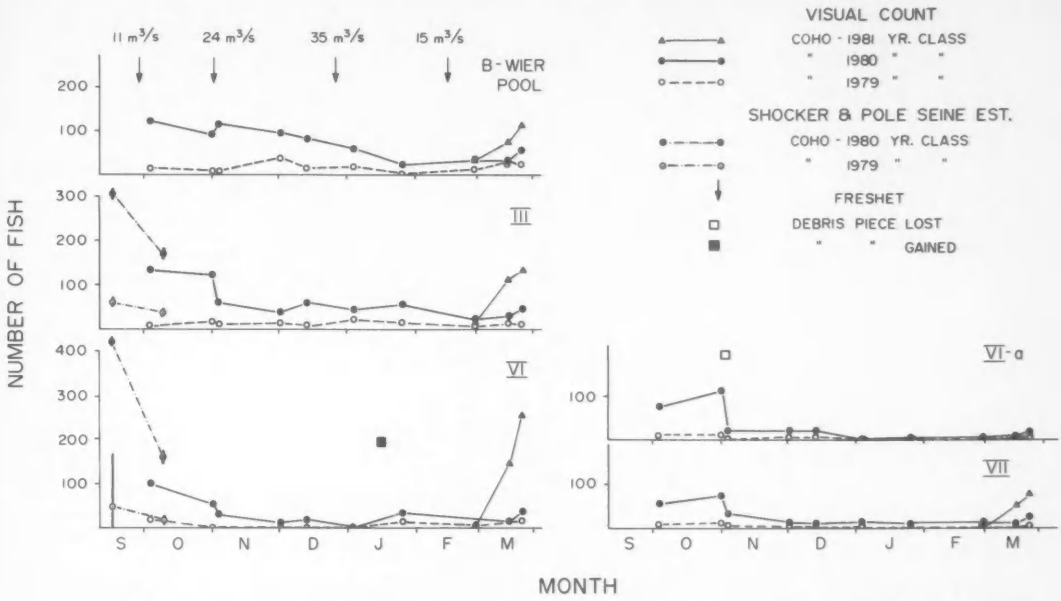


FIG. 1. Numbers of juvenile coho (1979, 1980 year-classes) overwintering in five selected sections of Carnation Creek during the autumn–winter of 1980–81. In late winter, all sections included some new coho fry (1981 year-class). Coho population sizes estimated by the Seber-LeCren (1967) removal method (sections III and VI, Sept. and Oct.) are given with 95% confidence limits (vertical lines). Arrows indicate freshet maxima.

ENUMERATION OF COHO OVERWINTERING IN SLOUGH AND TRIBUTARY HABITATS

Screen weirs, as described by Bustard and Narver (1975a), containing both "upstream" and "downstream" traps were constructed at the confluences of two side-channel sites with Carnation Creek. The traps at the 750-m site were checked from September to June each year from 1972 to 1981 except for March–June 1979 and January–June 1980, when no traps were operated. Traps at 1600 Tributary were operated only in 1972–73, 1973–74, and 1980–81. Observations were made daily except when flood conditions made observations impossible or when periods of drought occurred and the traps were thus dry. In several instances, trapping was suspended for a number of days when the weirs and traps needed repair.

The daily numbers of coho fry and yearlings entering the 750-m site and 1600 Tributary from Carnation Creek, and those leaving these areas, were recorded for each observation. Fish were removed from the traps and then anesthetized in a 1:4000 aqueous solution of 2-phenoxyethanol. Fork length of each fish was measured (from the tip of the snout to the tail fork), and scale samples were occasionally collected from fish >65 mm long to confirm the age of larger individuals. Simultaneously, water depths at each weir were read directly from staff gauges, and water temperatures in both sites and in Carnation Creek were taken with simple mercury thermometers.

Results and Discussion

MICROHABITATS OF COHO JUVENILES OVERWINTERING IN THE MAIN CHANNEL OF CARNATION CREEK

Observations made while enumerating coho revealed that microhabitats selected by coho fry and yearlings in winter were unchanged from those described qualitatively before logging by Bustard and Narver (1975a, b). Areas jammed with logs, undercut banks, and deep pools filled with upturned tree roots and other forest debris contained almost all the coho salmon that remained in the main channel of Carnation Creek during the winter. During winter (Nov.–Feb.) no coho were observed in midstream locations in any section, and coho did not inhabit areas under banks unless these sites contained tree roots and (or) lodged debris.

Consistent with the observations of Bustard and Narver (1975a) yearlings were often found deeper under banks than were fry. The former also occupied the deepest parts of pools (e.g. water depths ≥45 cm) more frequently than the younger coho.

All microhabitats occupied by fry and yearlings were characterized by low water velocities. Water velocity measurements taken at sites inhabited by coho juveniles revealed that all fish were found in water velocities <0.3 m/s. These largely qualitative findings are consistent with those reported in detail by Bustard and Narver (1975a, b).

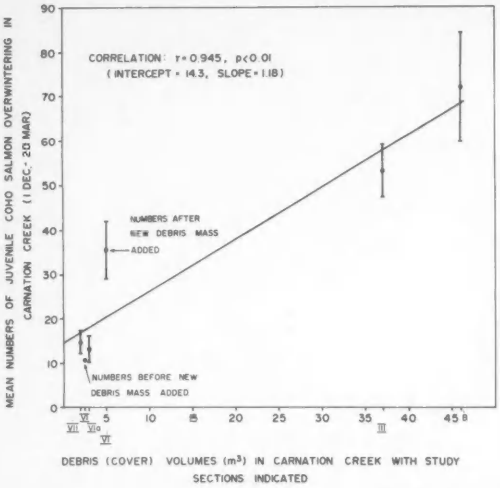


FIG. 2. Relationship between debris (cover) volumes and mean numbers of coho overwintering in five selected sections of Carnation Creek. Each mean (except those for section VI) represents seven individual enumerations from December 1 to March 20 when population numbers were relatively stable. Two means are given for section VI. One represents fish numbers before the addition of new cover in the form of a large root mass (Dec. 1–Jan. 3). This value results from only three enumerations and thus contains no ± standard error bars. The second value represents fish numbers after the root mass fell into the stream section.

SEASONAL REDUCTIONS IN THE NUMBERS OF COHO INHABITING THE MAIN CHANNEL

Coho population numbers in Carnation Creek are reduced substantially in winter compared with numbers inhabiting the same mainstream areas in summer (Fig. 1). Population estimates in sections III and VI revealed that most of this seasonal reduction occurs early in autumn (late Sept. and Oct.), coincident with the onset of freshets and low water temperatures (Fig. 1). For example, numbers of fry after the 11 m^3/s freshet of September 28 were reduced by about 63% in section VI and 45% in section III. Similarly, numbers of yearlings in the same sections were reduced, respectively, by 74 and 40%. Losses of fish in the clear-cut section VI, which contained little cover volume (Table 1), were much higher than in the partly forested section III, which contained high cover volume (Table 1).

Four major freshets occurred during the season studied. The first one (Sept. 28) was the least in magnitude but resulted in the largest declines in coho numbers in the two sections enumerated (Fig. 1, sections III and VI). Extreme discharge volumes such as those which occurred later in the season (Fig. 1) are thus not required to produce large numerical changes in the stream population early in the season. Subsequent freshets removed successively lower absolute numbers of fish from most study sections (Fig. 1); however, large declines in coho numbers continued to occur during the second seasonal freshet on November 1 (24 m^3/s). For example, the loss of most of one large root mass during the latter storm coincided with a decline in coho numbers from 122 to 23 in section VIa. Following the freshet of November 1, visual counts showed that coho populations in all sections fluctuated at low numbers (Fig. 1).

RELATION BETWEEN COHO NUMBERS AND HABITAT STRUCTURE IN MAINSTREAM SECTIONS

Sections containing winter habitat in the form of deep pools and undercut banks, both in association with tree roots and debris, lost fewer fish during freshets and maintained higher numbers of coho than sections without these features. For example, between the census of October 3, 1980, and the third (and most severe) seasonal freshet on December 26, 1980, coho juveniles were almost eliminated from two clear-cut sections of stream. No coho fry were observed in section VI. This section of shallow, relatively swift water contained almost no shelter of the form described above. Coho numbers in the adjacent section VIa (immediately upstream) were similarly reduced to one yearling. The freshet that occurred on December 26 eroded large areas of bank and caused its collapse in this section. Although section VII also occurred in the clear-cut zone of Carnation Creek, about 27% of the fry numbers and 29% of the yearlings counted on October 3 remained over the same time period. A stable debris mass located in a deep pool provided shelter for overwintering juveniles.

Sections III and B contained all of the features described above that gave shelter to overwintering coho. These sections contained streamside strips of trees, and most of the banks within these areas were stable. In addition, both sites contained stable debris in the form of submerged logs. Forty-eight and 32% of the fry numbers observed on October 3 in sections III and B, respectively, remained there on January 3, 1981.

Stream sections containing stable habitat and deep pools might have provided a refuge for fish displaced downstream from areas (e.g. section VI) where adequate habitat and cover were lacking. For example, section III contained over 4 times more yearlings on January 3 than were observed on October 3. Both sections III and B contained substantially more yearlings during winter than did any clear-cut section. Between-section movements of fish were also important in reestablishing at least low numbers of coho in sections VI and VIa by mid-to-late winter. Fish had virtually disappeared from both areas earlier in the season. The addition of a new root mass into section VI after a bank had collapsed coincided with an increase in population numbers, which stabilized at low levels from mid-January to late winter (Fig. 1).

During "mid-winter" (Dec. 1–March 20) when populations were relatively stable, the numbers of coho in each section were positively and linearly correlated ($r = 0.945$, $P < 0.01$) to the volume of debris present (Fig. 2). This relationship is based on limited data (only five study sections with numbers of fish in each section derived from seven enumerations); however, the data suggest that further investigation be undertaken. Future investigations must include a complete range of cover volumes in different study areas to

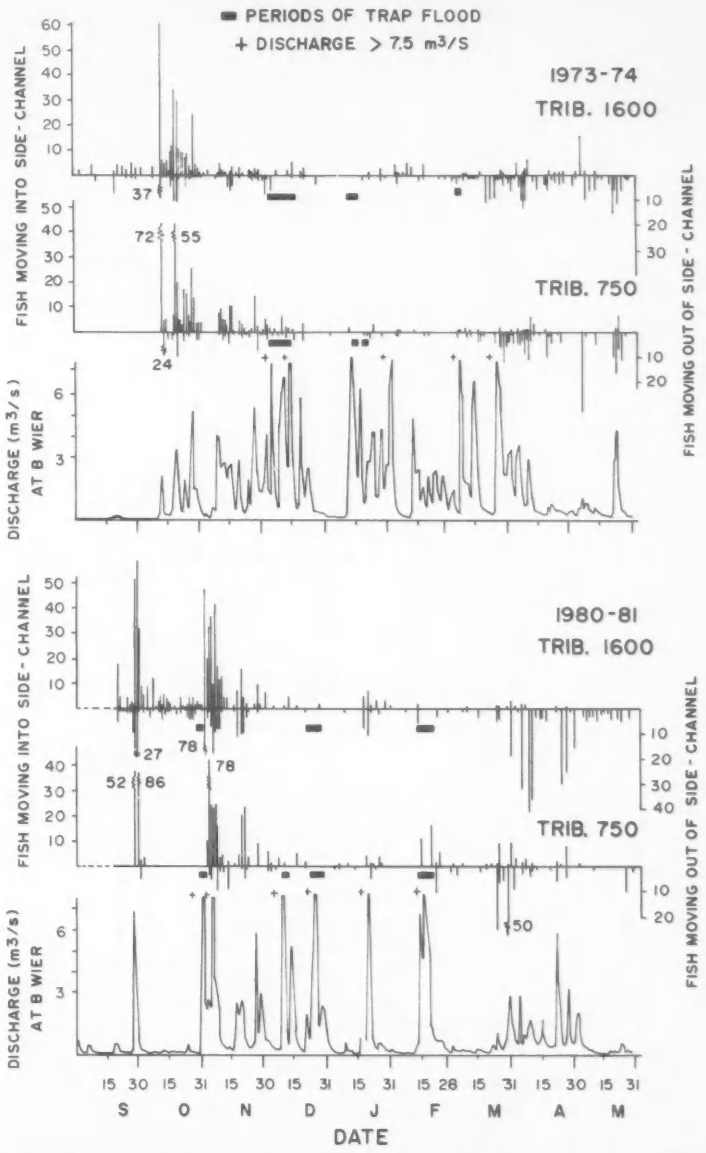
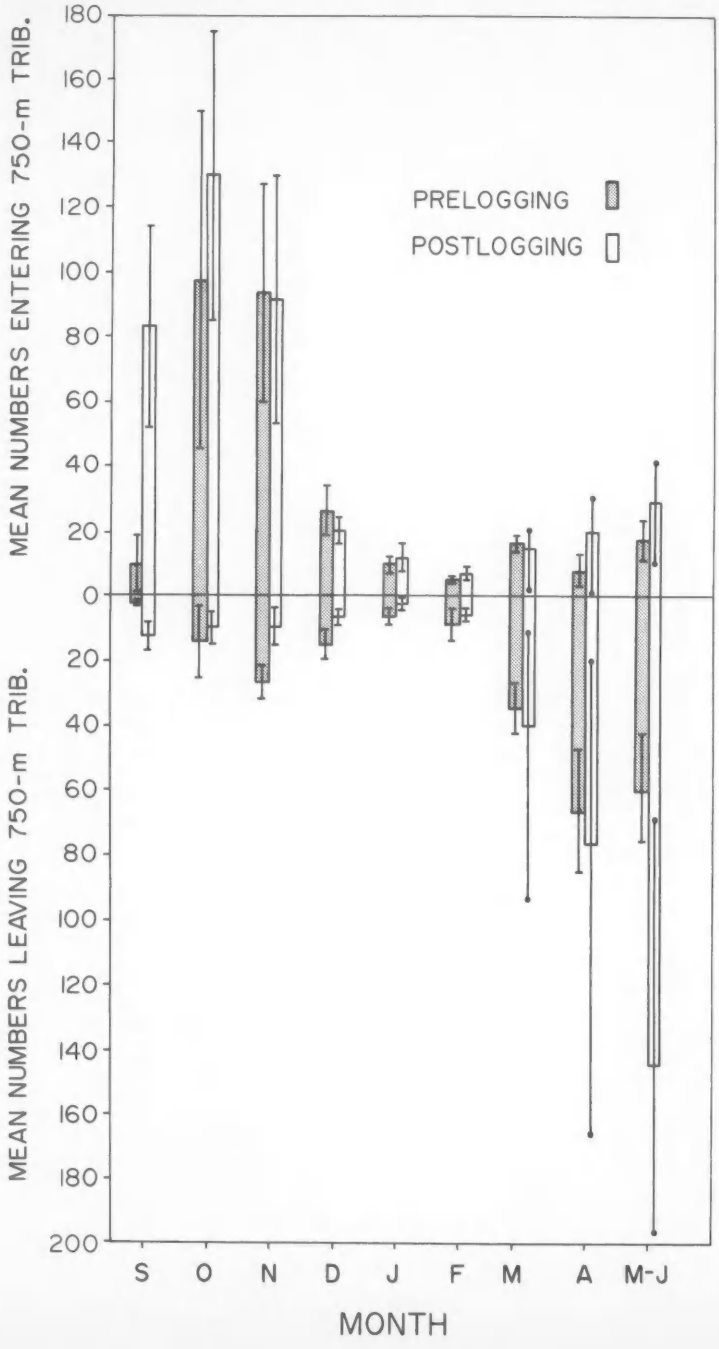


FIG. 3. Daily movements of coho juveniles (all ages combined) before logging (1973–74, top) and after logging (1980–81, bottom) between Carnation Creek and the overwintering sites at the 750-m slough and 1600 Tributary. Stream discharge volumes are also plotted (m^3/s). Traps could not always be checked during periods of heavy flooding. The symbol "+" is given when discharge volumes exceeded 7.5 m^3/s. Heavy solid bars indicate periods when traps were completely under water and thus not functioning properly.

establish a more detailed and precise relationship. Coho numbers were also correlated significantly to area of bank and debris cover ($r = 0.811$ and $P < 0.05$); however, the lower correlation coefficient for cover area demonstrates that much


MEAN NUMBERS ENTERING 750-m TRIB.
MEAN NUMBERS LEAVING 750-m TRIB.
PRELOGGING
POSTLOGGING
180
160
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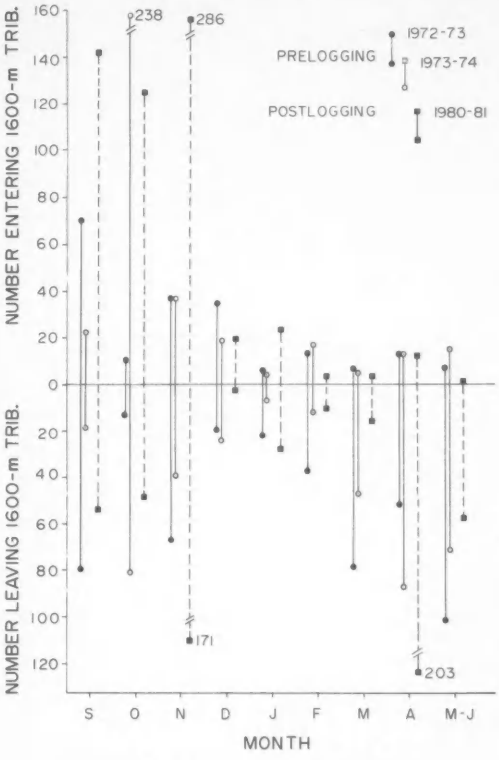

FIG. 5. Numbers of coho juveniles (all ages combined) overwintering in 1600 Tributary. Years before logging (1972–73, 1973–74) are represented by solid bars. A broken line represents 1980–81. Data are given as discrete annual values.

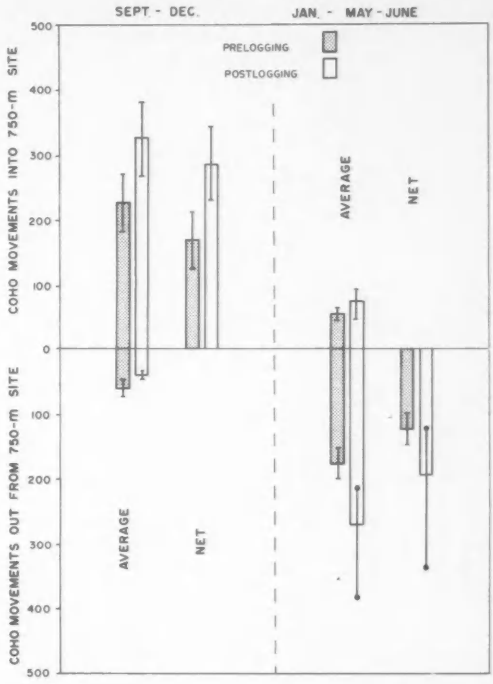

FIG. 6. Seasonal average and net mean movements of coho juveniles (all ages combined) into and out from the 750-m site. Shaded histograms represent prelogging years (1972–75). Clear histograms represent postlogging years (1976–81). Values are bounded by ± standard error bars except for January–May–June after logging. The latter means are bounded by their ranges because only 3 yr of complete seasonal data are available.

more of the variance in coho numbers and distribution is accounted for by cover volume than by cover area.

IMMIGRATION OF OVERWINTERING COHO INTO VALLEY SLOUGHS AND TRIBUTARIES

Three factors could account for the large reductions in coho numbers from the study sections in autumn: (1) mortality due to physical injury caused by freshets, (2) displacement of fish to locations downstream, and (3) immigration into valley sloughs and tributaries. The large reductions in the mainstream population in autumn coincided with the largest movements of fry and yearlings into the side-channel slough at 750 m and into 1600 Tributary (Fig. 3). Coho that left the main stream to overwinter in these sheltered habitats thus accounted partly for the low numbers inhabiting Carnation Creek during winter. However, the proportion of the total population that entered these areas is unknown because (a) not all sloughs and tributaries were studied, and (b) actual fish movements from one mainstream site to another could not be determined because fish were not marked for individual identification.

A general pattern exists in the seasonal movements of coho juveniles between Carnation Creek and its tributaries at 750 m and 1600 m: fish entered the tributaries in autumn and left them to reenter Carnation Creek in spring (Fig. 3). The largest movements of fish were generally coincident with peaks in discharge volumes in both spring and autumn

FIG. 4. Numbers of coho juveniles (all ages combined) entering and leaving the overwintering area at the 750-m site. Histograms depict mean movements into and out from the 750-m slough. Shaded histograms represent prelogging years (1972–75). Clear histograms represent postlogging years (1976–81). For September to December, means (with ± standard error) represent 4-yr prelogging and usually 5 yr when logging occurred. For January and February after logging, mean values (with ± standard error) represent only 4 yr of data because traps were not operated in 1979–80. For March, April, and May–June after logging, mean values represent only 3 yr because traps were not operated in 1978–79 and in 1979–80. The latter mean values are bounded by ranges.

(Fig. 3). No qualitative differences in the patterns of fish movements were detectable between the prelogging year of 1973–74 and the last year of logging (1980–81). The large daily movements into these side-channel sites in autumn occurred with the onset of the first seasonal freshets. These early peaks in stream discharge were usually much lower than those that occurred in midwinter. This phenomenon indicates that the autumn increase in discharge volumes may be a seasonal cue for coho to seek shelter before the extreme discharge volumes occur later in the year. Daily movements from December to February were generally low. From February to May, large movements out from the side-channel sites occurred (see monthly and seasonal data, Fig. 4, 5, and 6).

Large numbers of coho moved into the 750-m site from September to December during both prelogging and postlogging years (Fig. 4). Movements were bidirectional but far fewer fish reentered the main stream of Carnation Creek in this season. Large net movements of fish into the 750-m site occurred during autumn–early winter (Fig. 6).

In January and February, low numbers of fish moved in either direction between Carnation Creek and the slough at 750 m. Coho juveniles are relatively inactive in midwinter (Bustard and Narver 1975a; Hartman 1965). From late winter to spring, the net movements were reversed from those shown in autumn (Fig. 6). Overwintering coho left the 750-m site in large numbers and reentered Carnation Creek (Fig. 4 and 6). These seasonal shifts in distribution, first reported by Bustard and Narver (1975a) for early prelogging years, remained unchanged 5 yr after the first logging operations began in 1976.

When prelogging (1972–75) and postlogging (1976–81) periods are compared on a monthly basis from September to December, no clear differences in fish movements into the 750-m site are distinguishable except for September (Fig. 4). Large increases in coho movements into the site occurred after logging in that month (Fig. 4). This apparent increase may be due in part to sampling errors. Prelogging data were not collected for September in 1972 and 1974, and are incomplete for September 1973. Sampling problems notwithstanding, high between-year variation in the numbers of fish entering the 750-m site occurred for all months and thus renders prelogging and postlogging (including during logging) mean movements to be statistically the same (by analysis of variance) for October, November, and December (see ± standard errors, Fig. 4).

When monthly movements are combined to compare seasonal (autumn–early winter) net movements for prelogging and logging periods, new trends are shown (Fig. 6). The absolute numbers entering and leaving the 750-m site are statistically equal for both periods; however, a trend toward higher net movement of coho into the overwintering site occurred after logging began in 1976 (Fig. 6). However, this increase is not statistically significant ($P > 0.05$, by analysis of variance).

Similar relationships are shown for the January–June monthly and seasonal movements. Because traps were not operated in 1978–79 and in 1979–80, only 3 yr of data are available for March, April, and May–June after logging (Fig. 4). Prelogging and postlogging periods thus cannot be treated statistically for the latter months. However, monthly averages for movements both into the 750-m site and out from it were virtually the same except for May–June. Despite high between-year variation, a trend toward higher numbers of coho leaving the 750-m site after logging occurred for March and April and became more pronounced in May–June (Fig. 4). This trend resulted in higher seasonal (January–June) net movements of coho out of the 750-m site after logging began (Fig. 6). Although statistical comparisons (by analysis of variance) are not possible for this season, it is clear that logging has neither reduced the numbers of coho fry and yearlings that enter the 750-m slough in September–December to overwinter, nor reduced the numbers leaving the site to reenter Carnation Creek from January to June. In contrast, trends toward higher numbers of fish using the overwintering site are suggested.

An annual mean of about 169 ± 44 coho entered the 750-m site from September to December to overwinter before logging occurred in Carnation Creek. On the average, 122 ± 15 coho reentered Carnation Creek from January to June during the same period of time. If these net seasonal movements can be taken as a rough measure of overwinter "survival," then these values indicate a survival rate of 72.2% for coho using the site during prelogging years. From 1976 to 1981, annual numbers of coho entering the same site in "autumn" and then leaving in the "spring" were about 288 and 194, respectively. The survivorship rate for the postlogging period was 67.4%; little changed from the prelogging value. Although logging had removed the forest cover at the 750-m site, it appears that the quality of the coho overwintering habitat was not altered to the degree that overwinter survival of the fish was affected adversely.

The monthly and seasonal patterns of coho movements shown by the data for the tributary slough at 750 m are repeated at 1600 Tributary (Fig. 5). Only 3 yr of data are available for coho movements in 1600 Tributary (2 yr prelogging and 1 yr postlogging); however, these data are presented to illustrate that coho juveniles used similarly two different types of tributaries to overwinter. In contrast to 750 Tributary, which is frequently dry during spring and summer, 1600 Tributary is a more stable stream and has higher discharge volumes. No between-year differences can be distinguished in coho movements in 1600 Tributary (Fig. 5); therefore, no obvious logging-induced changes have occurred in the numbers of juvenile coho overwintering in the latter site (Fig. 5).

The seasonal movements of young coho described in this paper are consistent with those shown by Peterson (1980). He observed that many coho were displaced downstream during freshets in autumn. Some of these fish were able to enter tributaries, sloughs, and side channels to overwinter. These fish returned to the main stream in spring, during (or before) the period when stream-dwelling coho transform into seagoing smolts. Peterson (1980) documented that the downstream movement of coho in autumn can occur over long distances (hundreds of metres). The coho he studied overwintered in large, spring-fed ponds.

Implications Concerning Logging and Coho Salmon Habitat

This work and that of others (Bustard and Narver 1975a, b;

Peterson 1980) show clearly that valley tributaries and sloughs are essential for the winter survival of many young coho salmon. Conservation of these features is essential in habitat management efforts. These habitats should also be protected by forest-harvest planners and road-construction engineers. Forest-harvest planners and fisheries-protection specialists should also ensure that large, stable, debris masses (e.g. logs, tree roots), which occur normally in such streams as Carnation Creek, remain both during and after logging. Leaving a streamside buffer strip of trees after logging is important in the continued production of such debris. Streamside trees and other vegetation maintain the prelogging rate of bank erosion and reduce the potential for bank collapse.

Before logging, small numbers of adult coho and cutthroat trout (*Salmo clarki*) reproduced in 1600 Tributary. After logging, the channel became unsuitable for spawning because it had been filled with sediment and small debris (e.g. wood chips, tree bark). Given that adult fish spawn in such tributaries and that juveniles find refuge in them, forest-industry managers must ensure that they do not become obstructed by roads or blocked by undesirable materials.

Acknowledgments

Many people involved with the Carnation Creek Experimental Watershed Project contributed to this paper either directly or indirectly. We acknowledge all of these persons and express sincere gratitude to the following: Dr Blair Holtby, Dr Ian Birtwell, Dr John C. Mason, and J. Charles Scrivener for reading and criticizing the manuscript; Dick Leahy, Bruce C. Andersen, Philip Neaves, and Andrew Witt for construction of fish traps, monitoring daily fish movements, and collecting stream temperature and volume discharge data; and Helen Hartman and Shawn Mason for assisting in data collection and the recording of field observations.

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Evidence of Acidification of Some Nova Scotian Rivers and Its Impact on Atlantic Salmon, *Salmo salar*

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WATT, W. D., C. D. SCOTT, AND W. J. WHITE. 1983. Evidence of acidification of some Nova Scotian rivers and its impact on Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 40: 462–473.

River pH's in Nova Scotia are closely related to geology, and seasonal pH variation is well correlated with river discharge rates. In the geologically sensitive areas (granite and metamorphic rocks), river pH's have fallen significantly over the past 27 yr at an apparent average rate of 0.017 pH units/year. Concomitant with this decrease are a decline in HCO_3^- concentrations and increases in Al^{+++} and $SO_4^=$. On average, 73% of the increase in acid is attributable to increased $SO_4^=$. Changes in Na^+, K^+, Ca^{++}, and Mg^{++} concentrations were not significant. In rivers presently at mean annual pH's <4.7, the Atlantic salmon (*Salmo salar*) runs have disappeared and are presumed extinct. Rivers in the pH range 4.7–5.0 show a decline in salmon angling returns of 2.8%/yr, beginning about 1954, and low densities of juvenile salmon. Rivers presently of pH > 5.0 generally have normal juvenile densities and show no significant trend in angling returns.

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En Nouvelle-Écosse, le pH des rivières est en étroite relation avec la géologie, et les variations saisonnières le sont avec le débit des rivières. Dans les régions géologiques plus sensibles (granite et roches métamorphiques), le pH des rivières a baissé de façon significative au cours des 27 dernières années et cela à un taux moyen de 0,017 unités pH/année. Il s'est produit en même temps un déclin de concentration de HCO_3^- et un accroissement de Al^{+++} et $SO_4^=$. En moyenne, 73 % de l'augmentation de l'acide est attribuable à l'augmentation de $SO_4^=$. Durant la même période, il ne s'est produit aucun changement significatif des concentrations de Na^+, K^+, Ca^{++} et Mg^{++}. Les populations de saumons atlantiques (*Salmo salar*) ont disparu des rivières dont le pH annuel moyen est inférieur à 4,7 et sont présumées éteintes. Les rivières à pH de 4,7–5,0 montrent un déclin des prises sportives de 2,8 % par année à partir de 1954 et de faibles densités de juvéniles. Les rivières à pH supérieur à 5,0 ont en général des densités de saumoneaux normales et ne montrent aucune tendance significative des prises sportives.

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PRECIPITATION data available from Environment Canada's Canadian Network for Sampling Precipitation (CANSAP) indicate that the present annual mean pH of precipitation in Nova Scotia is in the range 4.4–4.6. This result contrasts with the mean of 5.7 determined from 24 mo of precipitation data reported by Herman and Gorham (1957) for Kentville, N.S., in 1952–54. Both of the above surveys used monthly bulk samples analyzed by glass electrode pH meters. Farmer et al. (1980) report a mean pH of 4.7 from individual precipitation events during the 18-mo interval from July 1978 to December 1979 at the Mersey Fish Hatchery (about 100 km southwest of Kentville). Also, Ogden (1980) reports that the mean pH of 10 precipitation samples collected at Kentville in 1977–78 was 4.7. It seems clear that the acid content of precipitation in Nova Scotia has increased by a factor of 10 or more since the 1952–54 period.

About one-half of the land area of Nova Scotia is underlain by granitic and hard metamorphic rocks (Fig. 1) of the type reported by Gorham (1957), Hayes and Anthony (1958), and Watt et al. (1979) as being associated with surface waters of low alkalinity (<0.05 mmol/L). The rivers and lakes of this area can be expected to show signs of recent acidification. An extensive pH survey in 1978–80 and a review of the National Water Quality Data Bank (NAQUADAT) and other existing data for surface waters in the Maritimes were reported by Watt (1981). These results confirmed a marked

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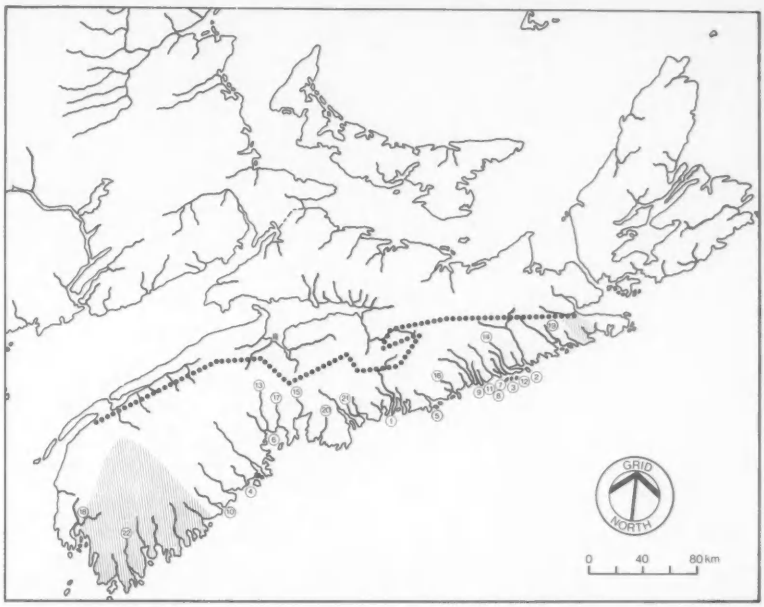

FIG. 1. Map showing the positions of the 22 Nova Scotian Atlantic Coast rivers with salmon angling records from 1936–1980. Rivers with 1980 pH's > 5.0 (1–12) are indicated by offshore numbers, and those of pH < 5.0 by numbers (13–22) placed inland. The numbering sequence is from Table 6. The dotted line indicates the contact between the granite or metamorphic rocks south of the line and the softer rocks to the north. The hatched areas are where river pH's in 1980 were < 4.7.

correlation between geology and pH, with severe acid conditions (pH < 5.4) restricted to that large area of granitic and metamorphic rocks on the Atlantic side of mainland Nova Scotia. This area has shallow soils and poorly developed drainages, including numerous lakes and many bogs and heaths. Metamorphic rocks in this region are the Meguma Series (Cambrian–Ordovician) which has two primary divisions: the Goldenville Formation consisting of greywacke and metamorphic equivalents, and the Halifax Formation which consists primarily of slate and which conformably overlies the Goldenville Formation. The granites in this area are part of an intrusive batholith of the Devonian (or early Carboniferous). Thirty-seven rivers known for Atlantic salmon angling flow through this region of Nova Scotia. In view of the increased acid loading from precipitation, we considered that a detailed monthly survey of river water chemistry would likely detect signs of recent acidification. Also, because the Atlantic salmon (*Salmo salar*) is known to be susceptible to low pH's (Daye and Garside 1977, 1980; Farmer et al. 1980), the salmon resources of this region could be showing signs of an acidification impact.

Methods

Measurements of pH in the field and laboratory were done with portable Metrohm model No. E588 pH meters following procedures recommended by Galloway et al. (1979). A comparison of field and laboratory measurements of pH showed no statistically significant differences. In dealing with hydrogen-ion data, the investigator can use either the (logarithmic) pH values or the hydrogen-ion activities (10^{-pH}). Preliminary statistical calculations demonstrated that the variance of 10^{-pH} is strongly heteroscedastic. This finding rules out the use of 10^{-pH} in variance analyses and related parametric statistical tests, because the probability levels estimated from such data would not be valid. The problem is that the magnitude of the variance of 10^{-pH} data rises with increasing values of 10^{-pH}. This phenomenon is common in biological and environmental chemical data, and the most commonly used solution is to transform the data, usually by taking the logarithm. For 10^{-pH} the obvious transformation is to use pH, the variance of which can be shown to be both additive and homoscedastic. To preserve the validity of the probability estimates, the pH format was used in all variance and covariance analyses, t tests, regressions, and correlations.

All other chemical analyses were performed (at the Environment Canada Water Quality Laboratory, Moncton, N.B.) on stored water samples employing techniques described by Environment Canada (1979): bicarbonate by double end point alkalinity titration; aluminum, calcium, and magnesium by atomic absorption spectrophotometer; sodium and potassium by flame photometer; sulfate by automated methylthymol blue colorimetry; and chloride by automated colorimetry with ferric ammonium sulfate and mercuric thiocyanate.

TABLE 1. Summary of 1 yr (1980–81) of monthly data from 23 Nova Scotia Atlantic Coast rivers classified as to the predominant bedrock geology of their drainage basins.

Predominant geology	Number of rivers	Mean pH 1980–81	pH range for group
Granite	4	4.81	4.44–5.37
Greywacke (Goldenville)	10	4.83	4.42–5.67
Slate (Halifax)	8	5.55	4.96–6.33
Limestone	1	6.64	

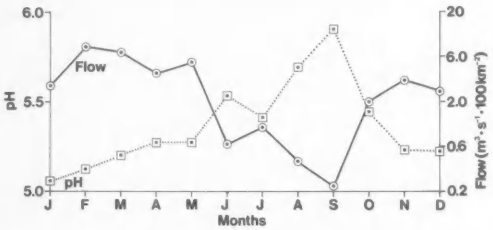

FIG. 2. The dotted line depicts mean monthly pH's (June 1980–May 1981) for seven rivers where sampling sites coincide with flow gauging installations. The solid line is mean (normalized mean daily) river discharge rates. The least squares equation is $pH = 5.501 - 0.459 \log \text{flow}$ ($r^2 = 0.834$, $P < 0.001$).

Electrofishing sites for juvenile Atlantic salmon density estimations were chosen with at least 50% riffle areas, and most sites averaged 18 cm in depth and 300–400 m^2 in area. Each site selected for electrofishing was enclosed by barrier nets. Shocked fish were captured by dip net and in a Pollet apron seine (Elson 1962). The elapsed time (usually near 30 min) for the initial pass was adhered to for succeeding passes. Generally five passes were made at each sampling site, with 10-15 minute breaks between passes. Estimates of fish density were calculated by the catch per unit effort method described by DeLury (1951).

The test statistics used were F ratios for the variance and covariance analyses where the numerator has multiple degrees of freedom; Student's t where the numerator has a single degree of freedom, when testing differences between pairs of means and for regressions; and r (or r^2) for correlations.

River pH's in 1980–81

In 1980, a monthly monitoring program was started for 23 rivers flowing into the Atlantic Ocean through Nova Scotia's zone of granitic and metamorphic rocks. Sampling sites (one per river) were chosen as near the mouths as practical (above tidal influence) so that the chemistry would be representative of entire primary drainages.

During the first complete year (June 1980–May 1981), the mean pH of these rivers ranged from 4.42 to 6.64. For statistical analysis the rivers were placed in four groups according to their predominant bedrock geology. The number of rivers in each group, mean pH, and group pH range are shown in Table 1. The data were subjected to a nested variance analysis

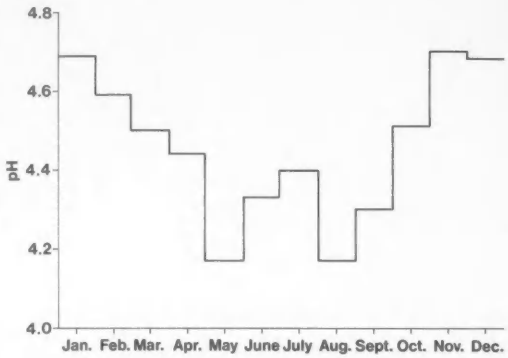

FIG. 3. Mean monthly pH of precipitation in Nova Scotia averaged (volume weighted) over three stations and 4 yr. The stations are at Shelburne, Kejimkujik, and Truro. Sampling was by monthly bulk samples. The data are from Environment Canada's CANSAP program for 1977–80.

to compare the differences between the geological groups with the differences between rivers within groups. There is no significant difference in mean annual pH between rivers on granite and those on the Goldenville (greywacke) Formation. The mean pH of rivers on the Halifax Formation is significantly higher ($P < 0.005$) than for rivers on granite or greywacke. The Halifax Formation is chiefly slates, and associated with the slate areas are clays (the natural product of weathering) and drumlin fields. The soil contained within the drumlins includes imported materials, possibly from sandstone areas (Triassic and Carboniferous) lying to the north. Clay has a high ion-exchange capacity which can provide buffering, and the imported soil in the drumlins is also relatively high in buffer capacity, thus higher pH's occur in the surface waters of these areas. The waters on granite, Halifax Formation and Goldenville Formation (22 rivers), are all significantly lower ($P < 0.005$) in pH than the one river (Musquodoboit) receiving drainage from a band of Carboniferous limestones that unconformably overlie the Meguma Series in its headwaters.

Variance analysis showed a significant ($P < 0.001$) seasonal (monthly) variation in pH, but the interaction between geology and season was not significant ($P > 0.05$), suggesting that the seasonal pH pattern in these rivers is independent of the mean annual pH level. The range of annual variation for the mean of the 23 rivers was 0.70 pH units (4.96 in January to 5.66 in September): the highest pH river (Musquodoboit) varied from 6.18 in February to 7.18 in September; the 14 rivers of minimum pH (on granite and greywacke) varied from 4.67 in January to 5.29 in September; and the eight rivers on slate varied from 5.25 in February to 6.09 in September. The apparent increase in the range of seasonal variation with increasing pH level may be coincidental only, as the correlation of range of seasonal pH variation versus mean annual pH for all rivers is not statistically significant.

The seasonal trend for all 23 rivers was similar to that depicted for the mean of 7 rivers in Fig. 2. Minimum pH

TABLE 2. Comparison of pH in 1954–55 with 1980–81 (data paired by months) by comparing means and testing differences in two-way variance analyses (a), and after correction for the correlation with the logarithm of river discharge rate (b). In (b), the pH's are calculated at geometric mean flows (G.M.F.) using least squares regressions, and significance levels are from analyses of covariance.

River:	Roseway	Medway	LaHave	Musquodoboit	Mersey
(a) Comparing means of pH's					
Mean pH 1954–55	5.30	6.07	6.22	6.97	5.94
Mean pH 1980–81	4.43	5.46	6.01	6.74	5.21
pH change	−0.87	−0.61	−0.21	−0.23	−0.73
Significance level	<0.001	<0.001	<0.05	ns	<0.001
No. of data pairs	13	7	12	7	13
(b) pH comparisons corrected for river discharge rate					
Mean flows (m^3/s)	9.13	16.0	17.6	4.80	
1954–55 $\hat{pH}$ at G.M.F.	5.23	6.09	6.26	6.97	No flow data
1980–81 $\hat{pH}$ at G.M.F.	4.44	5.43	5.99	6.73	
pH change	−0.79	−0.66	−0.27	−0.24	
Significance level	<0.001	<0.001	<0.01	ns	

occurred in midwinter, followed by a continuous rise until late summer and then a relatively abrupt decline to low winter values. This seasonal pattern is similar to that shown by 10 yr (1965–74) of monthly pH data from Tusket River (granite with greywacke), N.S., reported by Watt (1981). Additional data are available from the NAQUADAT file for Roseway (granite with greywacke), Medway (slate with greywacke and granite), and LaHave (slate) rivers for the period 1965–78. The Roseway River data (28 samples) show no apparent seasonal trend, but the Medway (117 samples) and LaHave (49 samples) data sets both show a marked trend toward low winter pH (minimum in December–January) and high summer pH (peaking in August–September), similar to Fig. 2. This seasonal pattern thus appears to be consistent from year to year[1] and river to river over a range of pH levels. On the Gold (granite), LaHave (slate), Liscomb (greywacke), Musquodoboit (limestone), Roseway (granite with greywacke), Sackville (slate with greywacke), and Medway (slate with greywacke and granite) rivers, the pH sampling sites coincide with flow gauges operated by Environment Canada. A joint regression of pH in 1980–81 versus the logarithm of mean daily discharge is significant ($P < 0.001$) and accounts for 78.6% of the within-river variation. Figure 2 depicts the mean monthly pH for these seven rivers and the mean monthly discharge which has been normalized by expressing discharge as $m^3 \cdot s^{-1}$ per 100 km^2 of drainage area. This normalization procedure gives equal weight to the flow data from each river. A high degree of correlation (inverse) is apparent from the graphs. Whereas the maximum annual pH in September coincides with the period of minimum annual flow, the minimum pH in midwinter precedes maximum flows (March–April) by 1 mo or more. This phenomenon was also noted by Watt (1981) for Tusket River (10 yr of monthly data) where minimum pH usually occurs in February and maximum flows are experienced in April. Watt was unable to explain this phenomenon, but suggested that it may be related to snow-melt conditions.

Since 1977, Environment Canada has been operating the CANSAP system whereby monthly bulk samples of precipitation are analyzed for pH and other major ions. Three CANSAP stations are located in Nova Scotia (at Shelburne, Kejimkujik, and Truro), and all three stations show a marked seasonal trend in pH of precipitation. Lowest pH's occur during the period May–September and highest pH's during November–February. This seasonal trend is illustrated in Fig. 3 wherein are plotted the monthly means of all pH data averaged over the three Nova Scotia stations and over the 4 yr 1977–80. Hornbeck et al. (1977), from the northeastern United States, and Farmer et al. (1980), from Mersey River, N.S., have reported a similar seasonal pattern. C. H. Castell (Fisheries Research Branch, Halifax, unpublished data) reports the same trend for the Halifax, N.S., area, and also reports that the lowest pH precipitation (<4.2) is borne on winds from the southwest sector, and highest pH's are from the north–northeast. The pH of fresh snowfall is significantly higher than that of winter rainfall, the difference being attributable to wind direction. During the winter months in Nova Scotia, winds are most frequent from the west–northwest sector, as cold air moves from the central Canadian Arctic towards the east coast. In summer, warmer air from the Tropics predominates and the most frequent wind direction is from the south–southwest sector (Gates 1975). Given the relative absence of pollution sources in the north as compared with the south (and especially the southwest), it is likely that this seasonal wind shift is alone adequate to explain the seasonal pH pattern of the precipitation. The relatively high pH of winter precipitation, especially of snow, in Nova Scotia, explains the pH rise in the rivers (Fig. 2 and Watt 1981) that occurs during the spring freshet.

This phenomenon has been further investigated by field observations during the January–February periods in 1981 and 1982. Six comparisons were made of midwinter snow

[1]For the period June 1981–May 1982, the monthly means of eight N.S. Atlantic Coast rivers reached pH maximum in August and minimum in December.

TABLE 3. The quality of past pH data for Medway River may be assessed by the fit (r^2) of the correlation with concomitant flow data. From a series of these regressions on flow (taking 2 yr of data for each), theoretical pH values were calculated at the mean annual flow (41.6 $m^3 \cdot s^{-1}$, from 65 yr of record) and these flow-corrected pH's can be regressed against years. Taking 1954 as year zero, the least squares equation is $\hat{pH} = 5.72 - 0.025$ (yr) and accounts for 80.3% of the variation in pH. A similar regression of average pH vs. years yields $pH = 5.93 - 0.030$ (yr) and accounts for 64.4% of the variation. Both regressions are significant to the $P < 0.01$ level.

Years of record	Number of samples	Regression on flow: r^2	Regression on flow: Significance level	Regression on flow: $\hat{pH}$ at 41.6 $m^3 \cdot s^{-1}$	Average[a] pH
1954–55	7	0.930	<0.001	5.8	6.1
1965–66	19	0.224	<0.05	5.5	5.7
1967–68	22	0.271	<0.02	5.3	5.3
1969–70	24	0.708	<0.001	5.3	5.4
1971–72	21	0.668	<0.001	5.2	5.3
1973–74	15	0.264	<0.05	5.1	5.1
1975–76	8	0.169	ns	—	5.4
1977–78	8	0.841	<0.01	5.2	5.4
1980–81	12	0.913	<0.001	5.2	5.3

[a]Converted to 10^{-pH} for averaging.

meltwater pH's with those in adjacent rivers (Barrington, Clyde, Sable, Medway, East, and Ingram rivers). In all cases the snow meltwater was substantially less acid, averaging 0.45 pH units higher than river water.

The mean monthly pH of precipitation is almost the inverse of the seasonal pattern of river pH's; the inverse correlation between mean monthly precipitation at the three CANSAP stations and mean monthly pH of the 23 monitored rivers is significant to the $P < 0.01$ level. The higher summer pH's in rivers are attributed to higher proportions of groundwater flow and biological alkalinity production.

Comparison with Earlier pH Data

The earliest known source of reliable (by present analytical standards) chemical data for Nova Scotia rivers is a 1954–55 survey reported by Thomas (1960). Thomas was concerned with suitability of the waters for uses in industrial processing. Glass electrode pH meters were employed, and so the pH measurements are directly comparable with present data. From the granite-metamorphic area of mainland Nova Scotia, Thomas (1960) reports on water chemistry from 12 rivers: 3 rivers were sampled approximately monthly over 1 yr (July 1954–June 1955), 3 were sampled about every 2 mo, and 6 were sampled once only. In the 1980–81 river chemistry monitoring program, three of the stations (Roseway, Mersey, and LaHave) correspond to Thomas' (1960) monthly sites and two (Medway and Musquodoboit) to bimonthly sites.

In the initial design of this study, it was considered that for the Roseway, Mersey, LaHave, Medway, and Musquodoboit rivers, data collected in 1980–81 in months corresponding to the 1954–55 data would be directly comparable and the differences statistically testable by variance analysis. The results of employing this procedure are reported in Table 2(a), which compares the mean pH's for 1954–55 with 1980–81 data. However, the strong correlation between pH and river discharge indicates that such a simple direct comparison is somewhat biased, as the flows in 1954–55 were different and on average higher than during the 1980–81 period.

A valid comparison must take into account the regressions of pH on stream discharge rates. For this comparison, separate regressions for pH on logarithm of river discharge were calculated for each time period, and, from these, representative pH's were calculated for each sampling period at the geometric mean discharge rate of the river (averaging over all sampling days and both data sets). These calculated pH's are presented in Table 2(b). The geometric mean flow was chosen as the point of comparison because pH's calculated at this flow will tend to coincide with the mean annual pH values. It would be feasible to use the regressions to correct all pH values for flow before statistical analysis, but this too would yield a bias probability estimate through failure to take into account the sampling error of the regressions. The statistical approach of choice was to use covariance analysis to compute corrected variance components for between years and for error, and the null hypothesis (i.e. when corrected for flows, pH's in 1980–81 were unchanged from 1954–55) was then tested by comparing the two corrected variance components (t test). The probabilities so calculated are reported in Table 2(b). There are no flow data for the Mersey River site, hence only Roseway, Medway, LaHave, and Musquodoboit can be corrected for flows in this manner. It will be apparent from Table 2, however, that the increased rigor obtained by applying flow corrections does not substantially alter conclusions as to the level of significance of the pH changes in these four rivers.

MacDougall and Cann (1961) report that during the late 19th and early 20th centuries, the Roseway River area was burned over repeatedly after lumbering operations. These fires destroyed soil organic matter and created the present-day extensive fire barrens with heath vegetation. The Roseway flows through the southern uplands of Nova Scotia. The land is a gently undulating plain sloping gradually to the south about 3 $m \cdot km^{-1}$. The area has many low ridges, often unforested (heath), between which are depressional areas usu-

TABLE 4. Mean concentrations (mmol/L) of ions in the water of four Nova Scotia rivers in 1954–55 and 1980–81.[a] Average differences were calculated as 1980–81 concentration minus 1954–55. The significance levels (except H^+) are from three-way variance analyses. The $SO_4^=$, Na^+, K^+, Ca^{++}, and Mg^{++} ions have been corrected for sea salt influence.

River	Years	Ion concentrations							
		HCO_3^-	$\frac{1}{2}SO_4^=$	Na^+	K^+	H^+	$\frac{1}{2}Ca^{++}$	$\frac{1}{2}Mg^{++}$	$\frac{1}{3}Al$
Roseway	1954–55	0.049	0.033	0.002	0.016	0.014	0.060	0.004	0.014
	1980–81	0.007	0.089	0.031	0.007	0.040	0.028	0.010	0.027
Medway	1954–55	0.055	0.031	0.016	0.006	0.001	0.047	0.016	0.007
	1980–81	0.013	0.059	0.018	0.005	0.005	0.045	0.017	0.014
Mersey[b]	1954–55	0.044	0.023	0.014	0.008	0.002	0.045	0.010	0.009
	1980–81	0.022	0.053	0.017	0.005	0.006	0.031	0.012	0.016
LaHave	1954–55	0.072	0.040	0.019	0.008	0.001	0.070	0.017	0.007
	1980–81	0.036	0.081	0.024	0.006	0.001	0.069	0.030	0.017
Average difference		−0.036	+0.039	+0.010	−0.004	+0.009	−0.012	+0.006	+0.009
Significance level		<0.001	<0.001	ns	ns	<0.001	ns	ns	<0.001

[a]The original data (uncorrected) are available on request from the senior author.
[b]Eleven data pairs; data from July 27 and Aug. 23, 1954 were not used because of lack of matching data.

TABLE 5. Quantities of acid (mmol/L) accounted for by changes (1954–55 vs. 1980–81) in mean concentrations within the river waters.

River	Acid attributable to:					% attributable to $SO_4^=$
	H^+	HCO_3^-	Al	(H^+ + HCO_3^- + Al)	$\frac{1}{2}SO_4^=$	
Roseway	+0.026	+0.046	+0.016	+0.088	+0.056	64
Medway	+0.004	+0.042	+0.006	+0.052	+0.028	54
Mersey	+0.004	+0.022	+0.009	+0.035	+0.030	86
LaHave	0.000	+0.036	+0.002	+0.038	+0.041	108
Means	+0.009	+0.037	+0.008	+0.053	+0.039	73

ally occupied by heath bogs and sluggish streams. The river water is dark brown (>100 Hazen color units in 1980–81). The river basin is inhabited only sparsely and agricultural and industrial activity is negligible. The underlying rock is mostly granite, with small areas of greywacke and its metamorphic equivalents and some slate. Soils are shallow and sharply layered.

The Mersey River is also on Nova Scotia's southern upland plain. Cann and Hilchey (1959) report that most of the river basin is covered with mixed forest, but a number of fire barrens with heath vegetation are also present and peat bogs are common. The river water is light brown in color (averaging 30 units). The predominant underlying bedrock is greywacke with areas of slate and granite. In greywacke and granite areas, the soils are thin, but in the slate areas there are numerous drumlins which have deeper soils. During the 19th century, the drumlin soils supported agricultural activity, but this use has now largely ceased. Except for a few kilometres near the mouth, the river basin is sparsely settled and the only substantial industry is forest harvesting. The river itself is extensively harnessed for power production (six mainstem dams).

The LaHave River basin is reported by Cann and Hilchey (1958) as 80% mixed forest. The underlying bedrock is largely slates and the area is covered by an extensive drumlin field. The drumlin soils support some agricultural activity, though this is not great in relation to the size of the basin. Peat bogs are common, and the waters are light brown (averaging 40 color units). The river basin is more heavily settled than the preceding two, but the population is concentrated near the mouth. Above the sampling site the only substantial industries are forest harvesting and minor agriculture.

The Medway River basin is adjacent and similar in topography and geology to the Mersey. The commonest underlying bedrock is slate with substantial areas of greywacke and granite. The basin is very sparsely inhabited and the only significant industry is in forest products, though previously there were active farms on the drumlin soils in the slate areas. The river water is light brown (averaging 40 color units).

The Musquodoboit River basin is underlain by granite, greywacke, slate, and a large area of Carboniferous limestone, gypsum, and evaporites. The Carboniferous rocks are overwhelmingly dominant in controlling water chemistry. Levels of calcium, magnesium, sulfate, and bicarbonate are 5–10 times higher in the Musquodoboit than in the preceding four rivers. Of the five rivers, the Musquodoboit Basin is also the most densely settled because of a thriving agricultural industry (on the Carboniferous soils) as well as forestry and

TABLE 6. A list of 22 Nova Scotian Atlantic Coast rivers for which salmon angling data are available from the past 45 yr. Rivers with substantial hatchery stocking, or major dam construction or removal have been excluded. Least squares regressions were calculated for catch vs. year and the regression coefficients tested with a t test.

River	Mean pH 1980–81	Regression of angling catch on year		
		Slope (salmon/yr)	% of variation accounted for	Significance level
1 Musquodoboit	6.7	−1.73	2.0	<0.01
2 St. Mary's	6.1	+6.88	6.2	ns
3 Ecum Secum	5.7	+0.43	1.4	ns
4 Petit	5.6	−1.61	7.2	ns
5 Ship Harbour	5.6	−0.41	2.0	ns
6 Gold	5.5	+2.17	1.4	<0.05
7 Moser	5.4	+1.04	2.1	ns
8 Quoddy	5.4	+0.03	0.0	ns
9 Kirby	5.4	−0.29	2.2	ns
10 Medway	5.4	−5.20	7.4	ns
11 Salmon (Port Dufferin)	5.3	+0.64	2.3	ns
12 Gaspereau	5.2	+0.37	6.0	ns
13 Middle	5.0	−1.37	59.6	<0.001
14 Liscomb	5.0	−1.26	6.3	ns
15 Ingram	5.0	−3.98	38.0	<0.001
16 Tangier	4.9	−2.27	29.1	<0.001
17 East	4.8	−1.30	69.0	<0.001
18 Tusket	4.8	−2.25	23.4	<0.01
19 Isaacs Harbour	4.8	−0.55	17.1	<0.02
20 Nine Mile	4.8	−0.77	38.6	<0.001
21 Salmon (Lawrencetown)	4.7	−1.98	45.5	<0.001
22 Clyde	4.6	−1.25	31.2	<0.001

mining. Considerable development has occurred within the basin over the past 26 yr, hence it is difficult to assign chemical changes to any one cause.

The NAQUADAT data from 1965 to 1978 can also be included in this examination of the rate of acidification. However, for the Roseway and LaHave rivers, the available data are judged unreliable as a result of an absence of significant correlation between the reported pH's and the concomitant river discharge rates, since the 1954–55 and 1980–81 Roseway and LaHave river data sets are significantly correlated with flows. For Medway River, the data available are from 1965 to 1978, and these may be compared with the earlier and present data (Table 3). The correlations with river discharge rates are generally lower for the NAQUADAT data than for the 1954–55 and 1980–81 data sets, but only 1975–76 is below significance level. To compare all data (1954–81) from the Medway site, each regression of pH on the logarithm of the discharge rate was used to calculate the representative pH at the mean annual flow (calculated from the total 65 yr of record), and these are reported in Table 3. The mean annual flow is higher than the geometric mean flow used for the calculations of Table 2(b), and corresponds approximately to the average flow conditions during the latter half of the month of May.

Farmer et al. (1980) have shown that for Atlantic salmon the most acid sensitive phase of the life cycle is the early feeding stage, after yolk sac absorption, which in Nova Scotia's Atlantic Coast rivers would usually occur in late May, at which time river discharge rates are usually near the mean annual values. For evaluating the impact of pH reduction on the salmon resource, therefore, it is convenient to use the mean annual flow calculated from a long period of record as the reference flow for year-to-year pH comparisons. The least squares regression of Medway River pH at mean annual flow (41.6 $m^3 \cdot s^{-1}$) on years is significant ($P < 0.01$) and accounts for 80.3% of the pH variation. The slope (−0.025 pH units/yr), may be compared with the pH changes for Medway (−0.022), LaHave (−0.008), and Roseway (−0.020) rivers, which have been calculated using only the 1954–55 and 1980–81 data, and using mean annual flow as the reference flow. The average for the three rivers is −0.017 pH units/yr, and this figure may be taken as an estimate of the average rate of pH decline in those Nova Scotian rivers that are entirely within the acid-sensitive area of granite and metamorphic rocks.

Other Chemical Data

Examination of the concentrations of other major ions permits a judgment about how the increase in hydrogen-ion concentration has occurred. Thomas' (1960) data allow comparisons to be made for calcium, magnesium, sodium, potassium, aluminum, bicarbonate, sulfate, and chloride. The analytical techniques (Thomas 1959) are all comparable with the 1980–81 data, except possibly that for aluminum. Thomas' aluminum concentrations were measured colorimetrically using the ferron technique (with a correction for iron).

The proximity of these river basins to the North Atlantic

Ocean results in considerable input of seawater ions for which due allowance must be made. Using 1980–81 data and Thomas' 1954–55 data from Roseway, Medway, Mersey, and LaHave rivers, the analytical values for calcium, magnesium, sodium, potassium, and sulfate were corrected for sea salt contribution using the seawater chloride ratio, as per Watt et al. (1979), and the data for each of the five corrected ion concentrations and for aluminum and bicarbonate (the sea spray corrections for bicarbonate and aluminum are negligible and were not applied) were then grouped in three-way variance analyses (rivers, years, and months). This approach was not applicable to the Musquodoboit River data because of other apparent anthropogenic changes in water chemistry. In Musquodoboit River, the data show a significant calcium increase of 0.60 mmol/L and a sulfate increase of 0.62 mmol/L over 1954–55 levels, which suggests increased gypsum or anhydrite input from the waste of local quarry operations.

These statistical analyses indicate significant seasonal variation in magnesium, sodium, sulfate, and bicarbonate, but no significant changes since 1954–55 for mean concentrations of calcium, magnesium, potassium, or sodium. At the same time, bicarbonate shows a significant decline and aluminum and sulfate show significant increases, but the rivers/years interaction component is not significant, indicating that the change in concentration for these three substances was the same (within error limits) for all four rivers. Increases in hydrogen-ion activities are also significant. Mean values for ion concentrations in these rivers are presented in Table 4. The bottom two rows of Table 4 give average differences (1980–81 minus 1954–55) and levels of significance for these differences.

The increased mineral acid in the precipitation is represented directly in the river water by increased hydrogen-ion concentration and indirectly by reduced bicarbonate concentration and by increased aluminum concentration. Aluminum hydrolizes to form a series of hydroxides, dissociation constants for which are given by Naumov et al. (1974). The pK for each step of aluminum hydrolysis can be compared with the mean pH's of rivers in 1954–55 and in 1980–81 (as given in Table 2). From the dissociation constants and the pH's, estimates can be calculated of the relative proportions of the various aluminum hydroxides and so of the quantity of hydrogen ion attributable to acid neutralization by mobilized aluminum. Implicit in this correction is the assumption that the aluminum increases are entirely of Al^{+++} and its hydroxides. The results of these aluminum corrections for the four rivers are presented in Table 5. The hydrolysis corrected value for acid neutralization by aluminum at the relatively high pH of LaHave River water is +0.002 mmol/L of acid (H^+ equivalent) as compared with +0.010 for the uncorrected value, but this was the only substantial change that resulted from the correction for hydrolysis. The overall corrected mean is +0.008 (Table 5) as compared to +0.009 (Table 4).

Table 5 contains estimates of the concentrations of increased acid input attributable to increased H^+ and Al and to alkalinity (HCO_3^-) reduction, and compares the sums of these three to the accompanying increases in concentration of $SO_4^=$. On average, 73% of the increase in acid is attributable to increased $SO_4^=$.

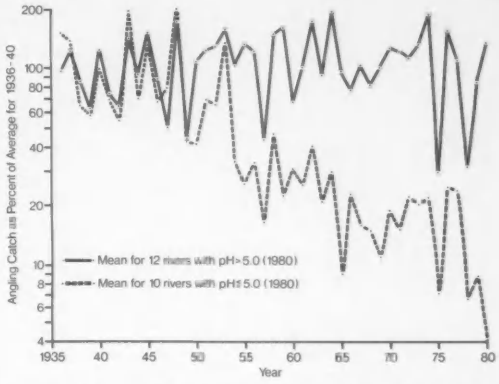

FIG. 4. Atlantic salmon angling data normalized to facilitate the comparison between high and low pH rivers. Each river's catch was expressed as a percentage of the mean catch in 1936–40 so as to give all rivers equal weighting, and the two groups were then averaged by year.

Tables 4 and 5 are interpreted as indicating an increased input of acid (mostly sulfuric) which has been largely neutralized by bicarbonate loss and aluminum mobilization. There is no evidence for any significant increment in the production of acid neutralization capacity from dissolution of carbonate base minerals (Ca^{++} or Mg^{++}) or from cation exchanges other than with Al^{+++}.

If the total change in bicarbonate, aluminum (after hydrolysis correction), and hydrogen-ion concentrations is a valid estimate of the increase in acid, then since 1954–55 the average increase in these four rivers is 0.053 mmol/L. This estimate can now be compared to the difference between Herman and Gorham's (1957) precipitation data from 1952 to 1954 and present Nova Scotia precipitation pH data. The pH decline in the precipitation is from 5.7 (weighted mean for Kentville in 1952–54) to 4.4 (weighted mean for Shelburne, Kejimkujik, and Truro in 1980). Because 5.7 is near the expected equilibrium value for water in equilibrium with air of normal CO_2 content, the 1952–54 value indicates a negligible content of strong mineral acids. For 1980 precipitation data with a pH of 4.4, it may reasonably be assumed that virtually the entire acid content of 0.040 mmol/L consists of strong mineral acids. Allowing for a concentration effect of 35% (calculated from a 55-yr data record for runoff and precipitation in the Halifax area) from transpiration and evaporation would suggest that, as a result of acid loading from the precipitation, Nova Scotia's rivers should theoretically have increased their acid content by about 0.06 mmol/L. It would seem, therefore, that the increased acid content of the precipitation is entirely accounted for in the surface runoff.

Salmon Angling Statistics

In Nova Scotia, rivers of pH less than 5.4 occur only in that portion of the province that is underlain by granitic and metamorphic rocks (Watt 1981). Rivers in this area of the province flow in a southerly direction to the Atlantic Coast.

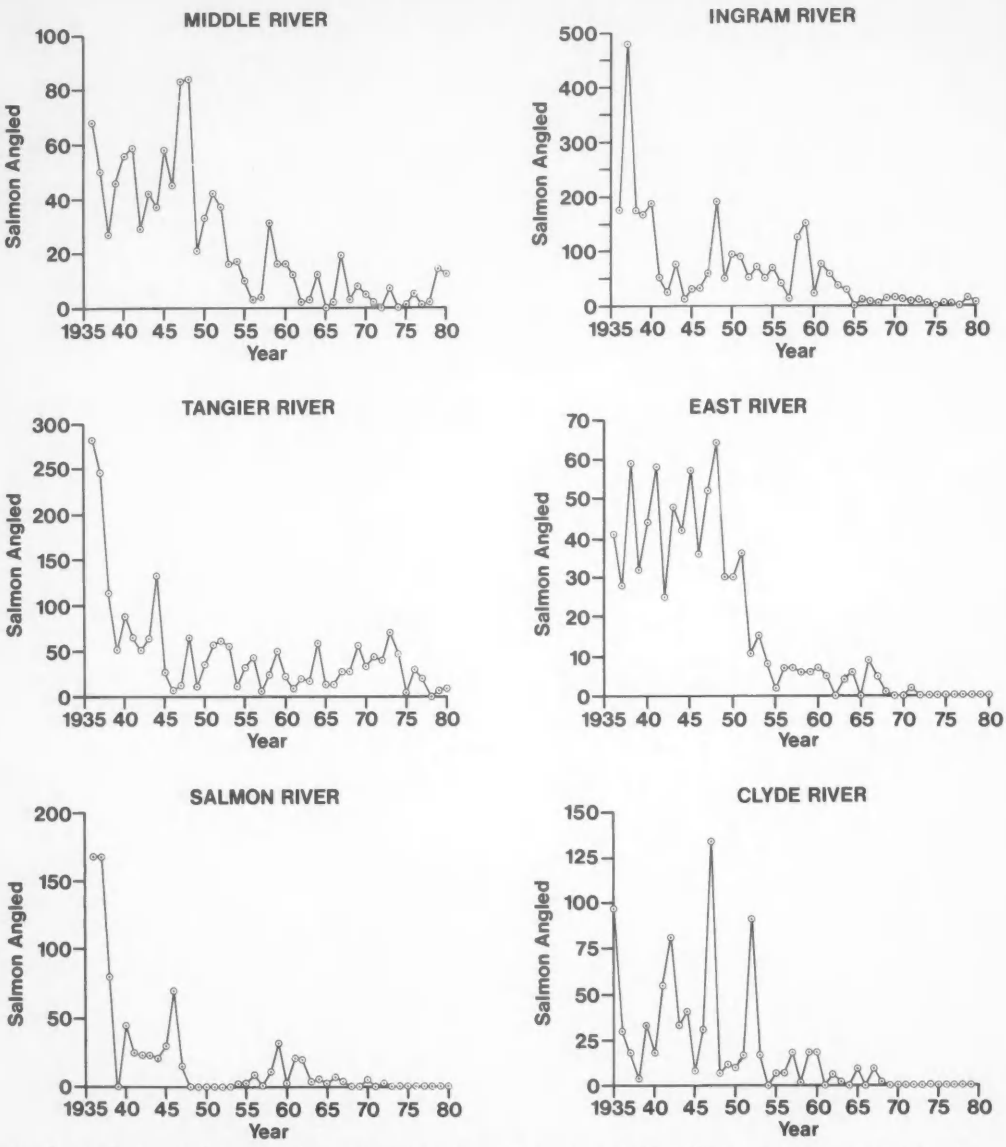

FIG. 5. Angling records for six Nova Scotia Atlantic Coast rivers with mean annual pH's (1980) ≤ 5.0. See Table 6 for further data.

There are 37 rivers flowing through this region which records indicate have had anadromous runs of Atlantic salmon. For 27 of these rivers, almost complete angling catch records are available in the annual reports of Federal Fishery Officers (18 districts) for the period from 1936 to 1980. Of these 27 rivers, five (Salmon River Digby, Mersey, LaHave, East Sheet Harbour, and West Sheet Harbour) have, during the ensuing period, undergone major dam construction or removal, and/or extensive hatchery stocking, and these have been excluded from further analysis.

The 22 remaining rivers are listed in Table 6, and their positions are indicated on the map in Fig. 1. To examine the impact of acidification on angling success, the 22 rivers were initially divided into two groups based on the average pH

TABLE 7. Atlantic salmon juvenile (fry and parr) density estimates (calculated from electrofishing data) for 19 Nova Scotia Atlantic Coast rivers. The rivers are arranged in order of mean pH in 1980–81.

River	Mean pH (1980–81)	Mean salmon/100 m^2	No. of site visits
Guysborough	7.0	33.7	2
Musquodoboit[a]	6.7	25.9	5
Salmon (Guysborough)	6.3	21.5	2
St. Mary's[a]	6.1	17.2[c]	51
LaHave (North Branch)	5.8	27.9[c]	7
Ship Harbour[a]	5.6	34.5	2
Medway[a]	5.4	35.6	5
Salmon (Digby)	5.2	16.5[c]	3
West	5.0	14.9	30
Sackville	5.0	3.7	4
Middle[b]	5.0	15.0	2
Ingram[b]	5.0	0.6	3
Tangier[b]	4.9	0.0	3
East[b]	4.8	0.5	2
Salmon (Lawrencetown)[b]	4.7	0.0	10
Tusket (East Branch)	4.6	0.0	4
Clyde[b]	4.6	0.0	3
Roseway	4.4	0.0	3
Sable	4.4	0.0	6

[a]See Table 6.
[b]See Table 6 and Fig. 5.
[c]Includes data from 1977 to 1979.

levels in 1980–81 using pH 5.0 as the dividing line; 10 of the rivers were at pH $\leq$ 5.0, and 12 were at pH $>$ 5.0. For the 12 rivers presently at pH $>$ 5.0; one (Musquodoboit) shows a significant decline in angling success, another (Gold) shows a significant increase, and 10 show no significant trend in angling returns over the 45 yr of record. The decline in angling returns from the Musquodoboit River is clearly not related to acidification (pH 6.7), and other evidence suggests that the causal factors are related to increased agricultural and industrial activities in this drainage basin. There is no obvious environmental cause for the apparent increase in angling success on the Gold River. The summed angling returns for all 12 rivers (Fig. 4) show no significant trend. It is notable in these data that the year-to-year variation in angling success is considerable. This appears to result from a combination of biological and psychological factors in that reports of good catches tend to encourage more anglers, and this in turn elicits more surveillance by Fishery Officers and higher catch reports. Conversely, a poor run or poor angling conditions discourage anglers and surveillance is more relaxed, all of which lead to lower catches and reduced accuracy of reporting. Because all of the rivers are in a confined region (the Atlantic Coast of Nova Scotia is about 500 km long), the biological or physical factors leading to greater or lesser angler success (e.g. sea survival, river discharge rates, or juvenile year-class survival) tend to act uniformly over the entire area. Hence, years of high angler success tend to be high in all rivers of the group, and similarly with low success years.

For the 10 rivers with mean 1980–81 pH's $\leq$ 5.0, the contrast with the higher pH group is striking. Nine show statistically significant declines in angling success and one shows no significant trend. Individual angling records for six of these rivers are depicted in Fig. 5. As with the 12 higher pH rivers, the year-to-year variation in reported angling catch is considerable. An examination of the individual river angling records for the Ingram, Salmon, and Tangier rivers (Fig. 6) suggests sharp declines in angling catches over the 1936–45 period, whereas the data from East, Middle, Clyde (Fig. 6), and Tusket and Nine Mile rivers suggest no trend until the late 1940s and then declines in the 1950s. The angling records for single rivers are not good guides to the past status of the salmon stock, because individual rivers are overly subject to changes over the years in angler preferences, and in levels of surveillance by Fishery Officers and reporting errors due to personnel changes. A somewhat more accurate picture of overall angling trends and stocks status for the region can be obtained by averaging the data from all rivers within each group.

The angling data were normalized, before averaging, so as to facilitate the comparison between the high and low pH rivers; and to allow each river to contribute equally to the average (two rivers have much higher catch records than the others). The procedure adopted was to express each river's angling catch as a percent of the average catch for the first 5 yr of record (1936–40) for that river. These percentages were then summed and averaged for each of the two pH groups and the results, presented graphically in Fig. 4, provide a rather dramatic picture of the impact of acidification on the Atlantic salmon. For both groups the year-to-year variation is considerable, reflecting the many factors affecting angling success and reporting accuracy. There is, however, a notable correspondence of high and low success years between the two groups, and the two curves are virtually synchronous until about 1950. Because the angling catch statistics for these rivers involve separate reports from a min-

imum in any 1 yr of 14 fishery officers, the degree of correspondence is a little surprising. Even after divergence in the 1950s, there is still a notable correspondence between low and high angling success years in the two groups of rivers. The logarithms of the angling returns for the two groups of rivers are significantly correlated ($P < 0.001$, $r^2 = 0.87$). In addition, of course, there is the obvious downward trend in angling returns from the rivers of low pH, which can be taken as an indication of the rate of impact of the acidification of these rivers on the Atlantic salmon resource.

A comparison of the two curves in Fig. 4 suggests that the rate of decline in the low pH rivers has not been continuous, and that the acidified rivers do not show obvious divergence from the higher pH group until the 1950s. Begining in 1954, the two lines diverge significantly, and this date may be taken to indicate the onset of significant acidification impact in some rivers (i.e. pH's near or below 5) in 1950 and/or 1951 when the salmon returning in 1954 would have been in the acid-sensitive fry stage. For rivers of pH $\leq$ 5.0, a regression of log total catch on year for the period 1950–80 yields an average rate of decline of 2.8% per year ($P < 0.001$), and accounts for 58.0% of the variation in catch.

Major anthropogenic changes having been ruled out, it is difficult to assign the difference in angling trends between these two groups of rivers to any cause other than acidification. As can be seen in Fig. 1, both groups are well distributed along the coastline so that geographically either could be taken as a representative sample for the area. Also, it would appear from tag return data (unpublished internal reports of the Fisheries Research Branch, Halifax) that salmon stocks in this area all share a common marine migratory pattern to waters off Newfoundland and Greenland; hence even the possibility of coincidental changes in sea survival are ruled out.

During 1980–82, electrofishing surveys were conducted in 19 Nova Scotia Atlantic Coast rivers, and for three rivers additional data are available from 1977 to 1979. In Table 7, the mean 1980–81 pH of each river is given along with the average densities of juvenile Atlantic salmon (fry and parr) calculated from the electrofishing results. Eight rivers were of pH > 5.0 and 11 of pH $\leq$ 5.0. In the higher pH rivers (which include Musquodoboit, St. Mary's, Ship Harbour, and Medway from Table 6) juvenile Atlantic salmon of all age-classes were present in normal (relative to other Maritimes salmon rivers in northern Nova Scotia and New Brunswick) densities of 20–30 fish/100 m^2. The 11 lower pH rivers included the six whose angling records are depicted in Fig. 5. Juvenile Atlantic salmon were found in Middle, Ingram, and East rivers, but not in Tangier, Salmon (Lawrencetown), or Clyde. On rivers of pH 5.0 juvenile densities were generally low. No juvenile salmon were found in waters of pH < 5.0. In the case of East River (pH 4.8), the fish were encountered in a higher pH (5.2) tributary which appears to function as a natural refuge. In the lower pH portion of East River, 10 sites were electrofished without barrier nets, but no juvenile salmon were found.

The most acidified rivers in Nova Scotia are in the areas indicated (by hatching) on the map in Fig. 1, where the 1980 mean annual pH's were <4.7. There are seven such rivers (Barrington, Clyde, Roseway, Jordan, Broad, Sable, and Larry's) for which historic data exist to prove their previous status as Atlantic salmon rivers (until about 1960), though their pH's are now too low for juvenile salmon survival. Angling reports on these rivers are sporadic and for most the reporting has been discontinued, hence these "worse case" rivers (except Clyde) do not appear in Table 6. As a group, these rivers are typified by high color (>100 units) and high dissolved organic carbon (>10 mg/L). All are on greywacke or granite, hence they tend naturally to low alkalinities and so would have been extremely susceptible to the acidification trend in the precipitation. Because of their clustering in the southwestern end of Nova Scotia they would also have been among the first to be subjected to acid precipitation, as the southwest is the major source sector. It is likely that the normal mean annual pH of these rivers is near or only slightly above that of the precipitation (there is no net retention of cations). The response of this group of rivers to the increased acid in the precipitation was (see Roseway, Tables 2, 4, and 5) elimination of the alkalinity, aluminum mobilization, and a large pH decline. In view of their "front line" position and extreme vulnerability, these rivers would have been the first to show significant acidification. In this regard, it is notable that Thomas' (1960) Roseway River data yield a mean pH of 5.3 in 1954–55 even though the precipitation at Kentville only 2 yr prior, but 200 km further northeast, averaged 5.7 (Gorham 1957). Electrofishing at what would appear to be physically suitable juvenile salmon habitat sites in three of these rivers (Table 7) failed to encounter a single juvenile Atlantic salmon. It has been concluded that the salmon runs native to these rivers are now extinct.

General Discussion and Conclusions

The Atlantic Coast rivers of Nova Scotia have become more acidic over the past 27 yr in response to increased acid loading in the precipitation. The fall in river pH is not uniform, varying with the acid neutralization capacity of the various drainage basins. Seriously acidified rivers (pH < 5.4) are found only within an area of granite and metamorphic rocks which underlies about one-half of the Nova Scotia mainland on the Atlantic side. Alkalinities have declined, and aluminum and sulfate concentrations increased, but there are no significant changes in concentrations of sodium, potassium, calcium, or magnesium.

The total increase in acid content of the river waters was estimated by summing changes in hydrogen ion, bicarbonate, and aluminum (corrected for hydrolysis), and this increase was found to be largely (73%) attributable to the increase in sulfate concentrations. The total acid and sulfate contents of the runoff water are in apparent balance with the precipitation loading.

The highest acid loadings occur during the summer months, borne on winds from the south–southwest sector; winter precipitation (northerly winds) is significantly less acid.

River pH is very closely correlated (inversely) with flow; hence, in comparing pH's of different years it is necessary to allow for flow differences. The seasonal pattern for river pH's follows the seasonal pattern of discharge rates, and is thus almost the inverse of the seasonal precipitation pH pattern. River pH's are maximum in late summer when flows are lowest, and minimum river pH's occur in midwinter, before

the spring freshet when the melting of the relatively high-pH snow generally brings about a rise in river pH's.

Within the area of granite and metamorphic rocks the lowest pH's are found in rivers on granite and/or greywacke. The rivers in slate areas have, on average, somewhat higher pH's, which is probably attributable to acid neutralization capacity associated with the drumlin formations common in the slate areas. The highest river pH's in the area of granite and metamorphic rocks are found in those rivers with headwaters in areas of carboniferous sediments.

Seven of the rivers on granite and/or greywacke have negligible acid neutralization capacity and their mean annual pH's are on a level (pH < 4.7) similar to that of the precipitation. The Atlantic salmon runs to these rivers are now extinct. A number of other rivers in the pH range 4.7–5.0 have much reduced Atlantic salmon stocks and the angling records indicate a steady decline since about 1954. Within the same Atlantic Coast area there are also a number of rivers wherein mean annual pH's are still > 5.0. Angling records for these rivers generally show no significant trend over the past 45 yr and juvenile salmon are still present at normal densities.

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Sea Urchins in the Saint Lawrence Estuary: Their Abundance, Size-Structure, and Suitability for Commercial Exploitation[1]

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Quantitative transects were made at nine locations along the Saint Lawrence Estuary, Québec, to examine changes in the abundance and size-structure of populations of the green sea urchin, *Strongylocentrotus droebachiensis*, in relation to the estuarine gradient. Near the seaward extremity of the estuary, sea urchin densities are very high and small urchins are particularly abundant in shallow water. In contrast, midway up the estuary, small urchins are scarce in shallow water, probably because they cannot tolerate the periodic drops in surface salinities which occur there. Where urchin densities are high, urchin grazing severely limits algal production, and because of low algal food availability, the urchin growth rate is exceedingly low. In the Upper Estuary, urchin numbers are low and no urchins are found near the surface. There is feeble recruitment of urchins, and the near absence of urchins of intermediate size suggests that there is a high probability that juveniles are killed before they reach intermediate size. The urchin growth rate is accelerated because of the abundance of algae present, and below 10 m deep some juveniles survive through the intermediate size range. After they reach 40–50 mm in diameter, they can move up to the 2- to 10-m-depth zone and can tolerate the periods of hypo-osmotic conditions which occur there. Suitable populations for commercial use are most likely found where salinity or winter ice conditions reduce urchin numbers to a level permitting greater algal abundance and an elevated somatic and gonadal growth of the remaining urchins.

HIMMELMAN, J. H., Y. LAVERGNE, F. AXELSEN, A. CARDINAL, AND E. BOURGET. 1983. Sea urchins in the Saint Lawrence Estuary: their abundance, size-structure, and suitability for commercial exploitation. Can. J. Fish. Aquat. Sci. 40: 474–486.

Des relevés quantitatifs ont été réalisés sur neuf transects, de part et d'autre de l'estuaire du Saint-Laurent, en vue d'évaluer, selon le gradient estuarien, les changements dans l'abondance et la structure de population de l'oursin vert, *Strongylocentrotus droebachiensis*. À l'extrémité aval de l'estuaire, la densité d'oursins est très élevée, et les petits individus sont particulièrement abondants en faible profondeur. Par contre, dans la partie médiane de l'estuaire, les petits oursins sont rares en faible profondeur, vraisemblablement parce qu'ils ne peuvent tolérer les diminutions sensibles de salinité qui interviennent périodiquement. Là où il y a de fortes densités d'oursins, dans la partie aval de l'estuaire, leur broutage très sévère limite considérablement la production algale, et diminue en conséquence la biomasse disponible, ce qui résulte en un taux de croissance des oursins très bas. Dans la partie amont de l'estuaire, le nombre d'oursins est faible, et aucun n'est trouvé près de la surface. On constate ici un faible recrutement, mais l'absence quasi totale d'individus de taille intermédiaire suggère à une forte probabilité que les juvéniles périssent avant d'atteindre cette taille. Leur

[1]Contribution to the programmes of MAPAQ (Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec) and GIROQ (Groupe interuniversitaire de Recherches Océanographiques du Québec).

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taux de croissance est accéléré à cause de l'abondance d'algues, et à des profondeurs supérieures à 10 m certains juvéniles atteignent la taille intermédiaire. Lorsqu'ils atteignent un diamètre de 40−50 mm, ils peuvent migrer aux niveaux de 2−10 m, et tolérer les conditions hypoosmotiques qui interviennent à ces niveaux. Des populations appropriées à l'exploitation commerciale peuvent se rencontrer là où la salinité ou les conditions hivernales de glace réduisent le nombre d'oursins à un niveau tel qu'il permet le développement des algues, d'où une croissance somatique et gonado-somatique chez les individus ayant résisté.

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ECHINODERMS have large areas of epidermal tissue exposed to the external environment and lack a differentiated organ of osmotic or ionic regulation, and are considered to be stenohaline (Binyon 1966). Nevertheless, an increasing number of species is known to tolerate salinities below 20‰ (Binyon 1966), and a few species can survive salinities below 13‰ (Binyon 1976; Turner and Meyer 1980). Previous studies on the response of echinoderms to reduced salinities have considered such aspects as the rate of change of internal fluids when animals are subjected to a change in salinity, geographical variations in salinity tolerance, and the capacity for isosmotic intracellular regulation (Emerson 1969; Lange 1964; Lawrence 1975; Stancyk and Shaffer 1977; Stickle and Ahokas 1974). However, no study has examined the changes in abundance, population structure, and distribution pattern of echinoderms along a zone of transition from salt to fresh water as occurs in estuaries. There is no simple progressive decrease in salinity going up estuaries but rather a complex salinity distribution pattern due to various hydrographic processes. Typically, there is a stratification of the water column, with a downstream flow of fresh water at the surface and an upstream movement of salt water at greater depths (Weyl 1970). Tides, the Coriolis effect, and seasonal changes in freshwater discharge from rivers also have important effects on the salinity pattern.

Our objective was to examine what changes occur in populations of the green sea urchin, *Strongylocentrotus droebachiensis*, along the salinity gradient of the Saint Lawrence Estuary, Quebec. *Strongylocentrotus droebachiensis* is the most abundant invertebrate in shallow-water rocky communities along the Atlantic Coast of Canada, and through its intensive grazing activities plays an important role in the organization of the infralittoral community in this region (Breen and Mann 1976; Himmelman 1969; Himmelman et al. 1983a; Wharton and Mann 1981). We were also interested in what changes occur in the abundance of macroalgae in the infralittoral zone along the Saint Lawrence Estuary, as the abundance of the sea urchin changes. Finally, in response to recent interest in developing an urchin roe industry in Québec, we wanted to obtain information on recruitment rates, growth rates, and the abundance of commercial-sized urchins along the estuary, information pertinent to the potential for such an industry.

Study Areas and Methods

The Saint Lawrence Estuary (Fig. 1) is a large basin measuring 380 km in length. There are important freshwater additions from the Saguenay and other rivers along the north shore of the estuary, as well as discharge from the St. Lawrence River. Its separation from the Gulf of Saint Lawrence is at the level of the constriction at Pointe des Monts, where surface currents from the north coasts of the estuary and gulf converge and form a transverse current towards the Gaspé Peninsula (Forrester 1967). Most workers recognize two distinct regions, the Lower Estuary and the Upper Estuary (Brunel 1970; El-Sabh 1979; Neu 1970) separated at the level of the Saguenay Fjord. Here there is an abrupt diminution in depth, as the Laurentian Trough, a channel greater than 200 m deep extending into the estuary from the continental slope, terminates. The Saguenay River outflow causes a transverse current to the south shore. Most of the Upper Estuary is less than 60 m in depth. In the Lower Estuary surface salinities usually vary from 20 to 32‰, compared to >30‰ in the gulf. In the Upper Estuary there is a progressive decrease in salinity to Île d'Orléans, the upper limit to which seawater penetrates (Bewers and Yeats 1979; Greisman and Ingram 1977; Neu 1970; Kranck 1979). In addition, there is a general decrease in salinity from the north to the south shore of both the Lower Estuary and Upper

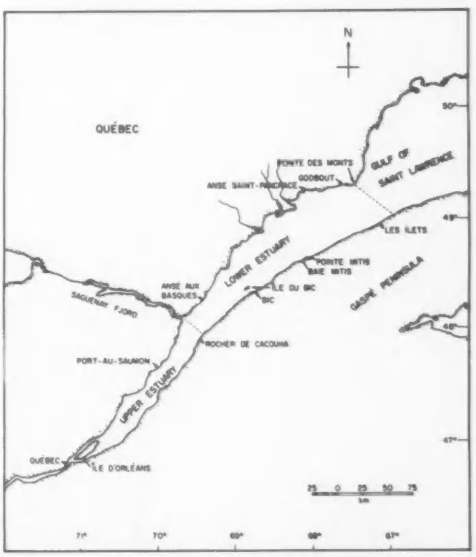

FIG. 1. Map of Saint Lawrence Estuary showing locations of study sites.

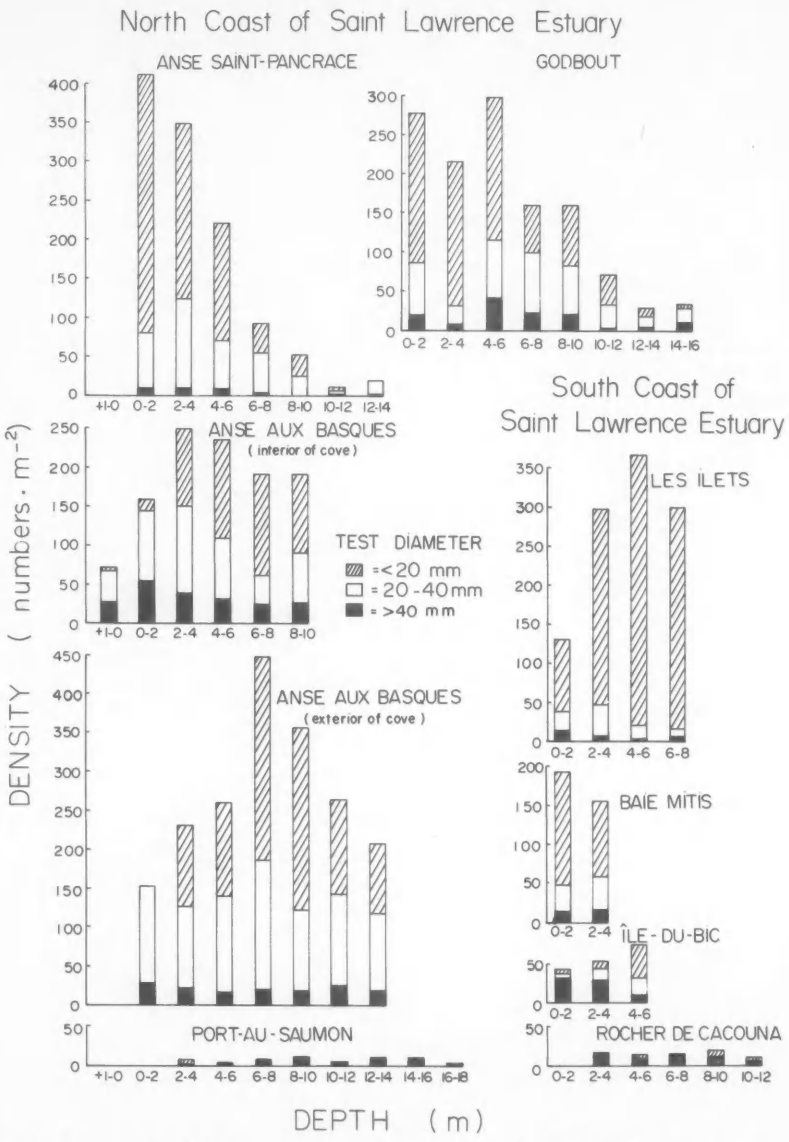

FIG. 2. Density of small (<20 mm in test diameter), medium-sized (20–40 mm), and large (>40 mm) urchins at different depths in the different transects on the north and south shores of the Saint Lawrence Estuary.

Estuary due to the Coriolis effect (Neu 1970). The Lower Estuary is relatively stratified (El-Sabh 1979). During the winter there is a layer with temperatures near 0°C and a salinity of 29–32‰ situated between 0 and 75–100 m in depth, and a warmer, more saline layer at greater depths. Because of solar heating and increased freshwater runoff, in the late spring and summer a third layer, which is warmer and less saline than the two deeper layers, develops at the surface to about 10 m deep. In the Upper Estuary, this stratification becomes destroyed, and the waters become well mixed approaching Île d'Orléans.

At nine locations in the estuary where the substratum in the

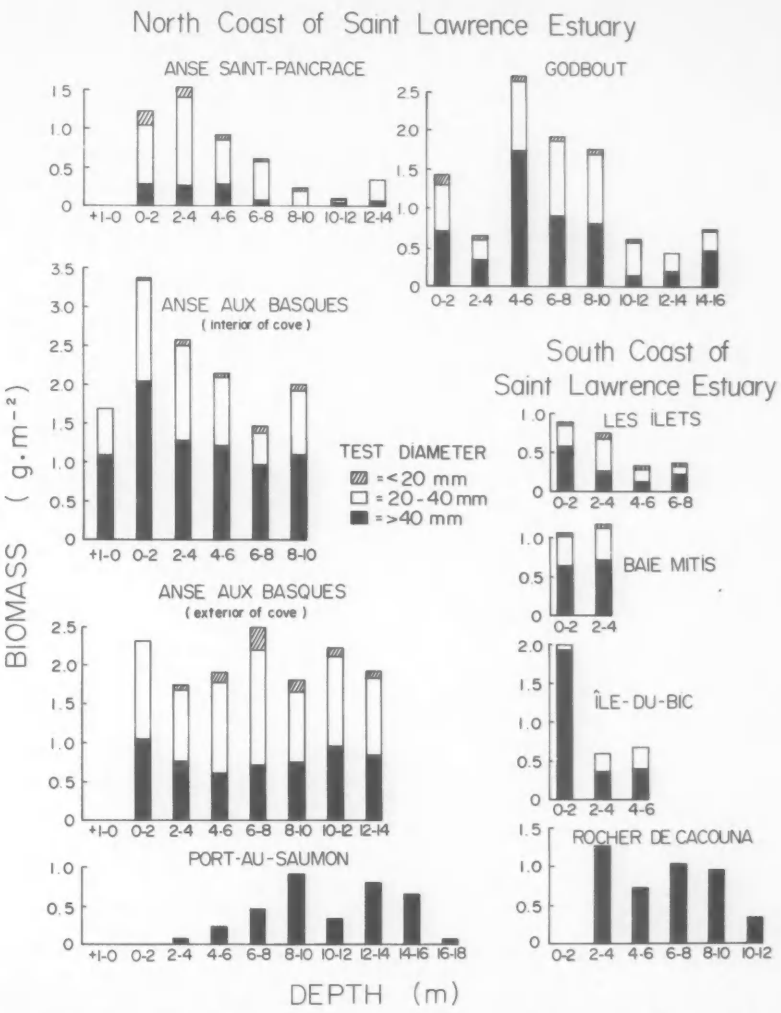

FIG. 3. Biomass of small (<20 mm in test diameter), medium-sized (20–40 mm), and large (>40 mm) urchins at different depths in the different transects on the north and south shores of the Saint Lawrence Estuary.

shallow water zone was rocky, vertical quantitative transects were made to examine the abundance and size-structure of urchin populations. Five transects were made along the north shore of the estuary: one at Godbout, one at Anse Saint-Pancrace, two at Anse aux Basques (one at the interior and one at the exterior of the cove), and one at Port-au-Saumon (Fig. 1). Four transects were made on the south shore of the estuary: at Les Îlets, Baie Mitis, Île du Bic, and Rocher de Cacouna. The distribution of these locations permits an examination of urchin populations related to the physical gradient of the estuary.

At each site a 100-m transect line, marked at 1-m intervals, was placed perpendicular to the shore. Pairs of divers, with the aid of scraping devices and an "air lift" apparatus, collected all organisms from 0.25-m^2 grids placed at predetermined positions along the transect line. The sampling procedure and "air lift" apparatus are described in detail by Himmelman et al. 1983b. At the beginning of each transect, samples were taken at 2- or 4-m intervals (depending on the slope of the shore) along the transect line from near low tide level to a depth where the rocky substratum terminated. Later, when we had good measurements of the depths along the transect line, additional positions along the line were sampled to give a more uniform number of samples for the different

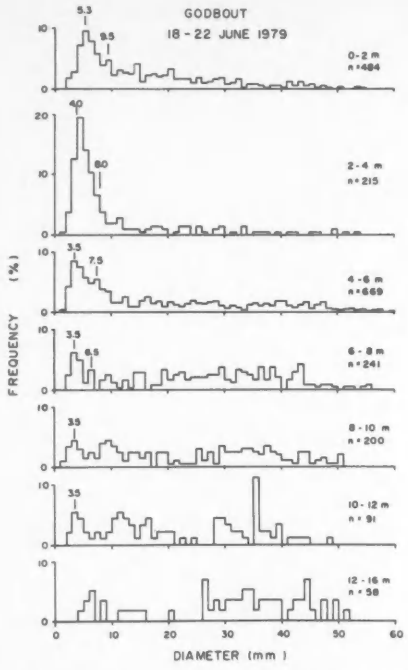

FIG. 4. Size–frequency distributions for urchins at different depths at Godbout. Numbers over histograms indicate positions of cohorts discussed in text.

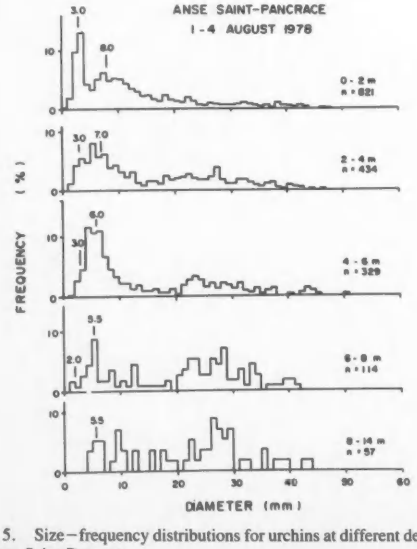

FIG. 5. Size–frequency distributions for urchins at different depths at Anse Saint-Pancrace.

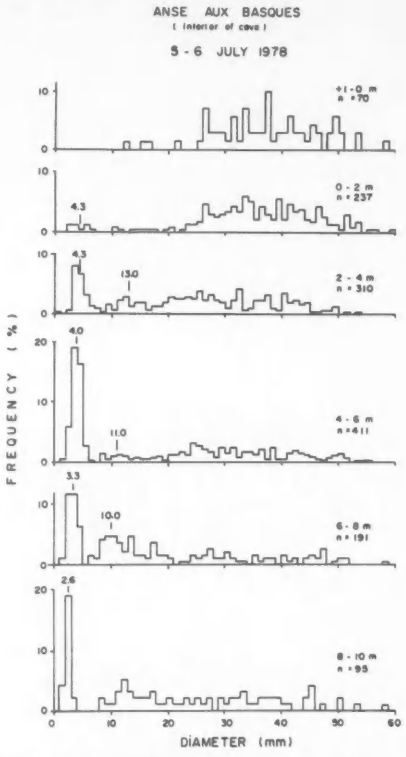

FIG. 6. Size–frequency distributions for urchins at different depths at the interior of Anse aux Basques.

depths along the transect line. Each transect took 4–5 working days, and the total number of samples per transect varied from 25–54.

Samples were sorted as soon as possible after collection (usually within 6 h). The diameter of all urchins was measured to the nearest 0.1 mm with vernier calipers. One measure was made of urchins measuring less than 30 mm in diameter and the mean of two measurements was recorded for larger urchins. Urchin biomass was calculated by regression from the diameter measurements, and our analysis of the rates of recruitment and growth in different regions in the estuary was based primarily on cohorts of small urchins identified from diameter–frequency distributions.

Results and Discussion

Density and Biomass

For the nine transects, the density and biomass of urchins are shown for each 2-m depth interval in Fig. 2 and 3. Near the entrance of the estuary at Godbout, a very high urchin density was found at 0–6 m deep; most of these individuals were less than 20 mm in diameter. At greater depths there was

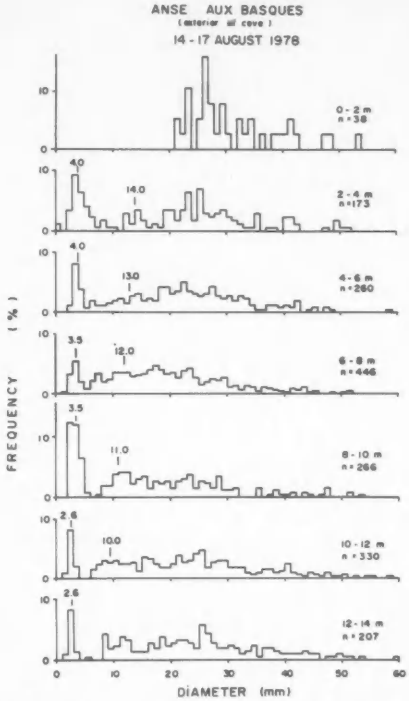

FIG. 7. Size–frequency distributions for urchins at different depths at the exterior of Anse aux Basques.

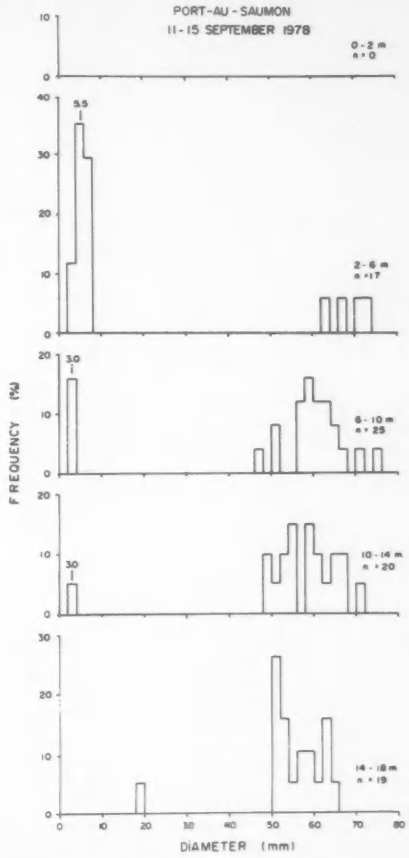

FIG. 8. Size–frequency distributions for urchins at different depths at Port-au-Saumon.

a decrease in density. Peak biomass occurred at 4–6 m deep; with increasing depth there was a general decrease in biomass. The drop in biomass observed above a 4-m depth, due to the decrease in numbers of medium-sized and large urchins, could be attributed to substratum differences. There was an inclined and relatively smooth bedrock slope above 4 m deep, and a relatively flat cobble bottom below 4 m deep. The larger urchins below 4 m deep most likely move to shallower water to forage when there are no wave conditions (Himmelman 1971, 1980). At Anse Saint-Pancrace, there was a similar decrease in density and biomass with increasing depth. The total biomass was generally lower than at Godbout because large urchins were less abundant.

Populations in the two transects at Anse aux Basques showed marked differences from those at Godbout and Anse Saint-Pancrace. There were low numbers of small urchins near low tide level. Further, there was a less-pronounced decline in urchin abundance with increasing depth, especially at the exterior of the cove where numbers of medium-sized and large urchins were remarkedly constant over the 14-m depth range sampled.

At Port-au-Saumon in the Upper Estuary the density of urchins was very low; no urchins were found at 0–2 m deep and at greater depths the density was very low. Most of the urchins present were large and as a result the biomass was not proportionally low.

At Les Îlets, the most seaward transect site on the south shore of the estuary, there were exceedingly high numbers of small urchins at 2–8 m deep (Fig. 2). The reduced numbers of small urchins at 0–2 m deep may be related to the dense algal cover at this level, as urchins are less abundant within *Laminaria* or *Alaria* beds (Breen and Mann 1976; Himmelman et al. 1983a). There was a decrease in the density of medium-sized and large urchins with increasing depth, and their numbers were lower than in the seaward transects on the north coast of the estuary (Fig. 2, 3). At 0–4 m deep at Baie Mitis, where there was a bedrock and boulder bottom, the population was similar to that at Les Îlets. Samples were not taken at greater depths, where the substratum was relatively flat and composed principally of gravel and sand, but we noted that medium-sized and large urchins were much less abundant than in shallower water.

In the inner part of the Lower Estuary at Île du Bic, the

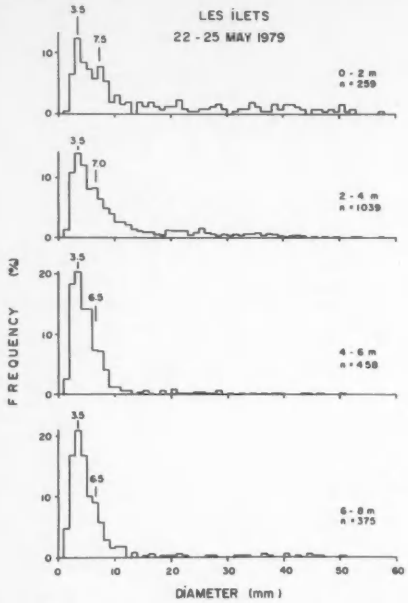

FIG. 9. Size–frequency distributions for urchins at different depths at Les Ilets.

urchin density was markedly lower than at Les Îlets and Baie Mitis as a result of low numbers of small individuals, particularly in shallow water. By contrast, large urchins were concentrated in shallow water.

There was a striking similarity between the population at Rocher de Cacouna, the innermost station along the south coast of the estuary, and that at Port-au-Saumon (Fig. 2, 3), there being no urchins at 0–2 m deep, and a low density of mostly large urchins at greater depths.

Thus, there were changes in the urchin populations at different locations going up the estuary which were seen on both shores of the estuary. In the seaward portion of the Lower Estuary, at Godbout and Anse Saint-Pancrace on the north shore and at Les Îlets and Baie Mitis on the south shore, the urchin density was high and small urchins were abundant in shallow water. Further up the estuary, at Anse aux Basques on the north shore and at Île du Bic on the south shore, small urchins were scarce at 0–2 m deep but increased in numbers with increasing depth. Finally, in the Upper Estuary at Port-au-Saumon and Rocher de Cacouna, there were no urchins in shallow water and at greater depths there were low numbers of mostly large individuals.

POPULATION STRUCTURE

In the size–frequency distributions for Godbout and Anse Saint-Pancrace on the north shore, there were strong modes of small individuals between 0 and 6 m deep but at greater depths small individuals were much less abundant and the size–frequency distributions were relatively flat (Fig. 4, 5).

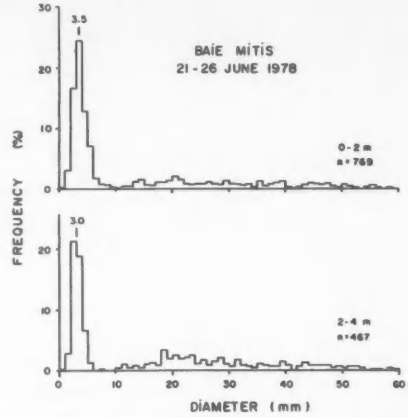

FIG. 10. Size–frequency distributions for urchins at different depths at Baie Mitis.

At Anse Saint-Pancrace (Fig. 5) a well-defined cohort of small urchins at 3 mm test diameter was evident at 0–2 m deep. This group was less well defined at greater depths. A second mode was suggested at 5.5–8 mm in test diameter. At Godbout (Fig. 4), the first group of urchins was centered at about 5.3 mm test diameter at 0–2 m deep, and at a slightly smaller size at greater depths. An older cohort was suggested at a size 3–5 mm larger. Thus, at Godbout and Anse Saint-Pancrace there were well-defined cohorts of small urchins indicating a high recruitment rate.

At Anse aux Basques there was a distinct group of small urchins centered at about 4 mm test diameter at 2–4 m deep and in a slightly less-advanced position at greater depths (Fig. 6, 7). A second group was suggested varying in position from 10 to 14 mm in test diameter. In marked contrast to Godbout and Anse Saint-Pancrace, at Anse aux Basques there was a broad group of large urchins, especially in shallow water. This group could represent an accumulation of year-classes, as has been described in urchin populations elsewhere (Ebert 1968; Leighton 1967), and suggests a lower rate of mortality at Anse aux Basques than at Godbout and Anse Saint-Pancrace.

At Port-au-Saumon, in spite of the very low density of urchins present, a unique size–frequency pattern was seen in the urchins present below 2 m deep (Fig. 8). A cohort of small urchins was evident, particularly at 2–6 m deep; there were no urchins of intermediate size; and there was a broad group of individuals larger than 46 mm in diameter.

A similar change was seen in the size-structure of urchin populations along the south coast of the estuary. At Les Îlets (Fig. 9) and Baie Mitis (Fig. 10), the size–frequency distributions closely resembled those at Godbout and Anse Saint-Pancrace in that cohorts of small urchins predominated. At Les Îlets the first cohort was centered at 3.5 mm diameter, and a second at 6.5–7.5 mm, whereas at Baie Mitis only one cohort at 3.0–3.5 mm was evident. In other sampling conducted 3.5 km to the east of Baie Mitis at Pointe Mitis (to be discussed in detail later), there was a second

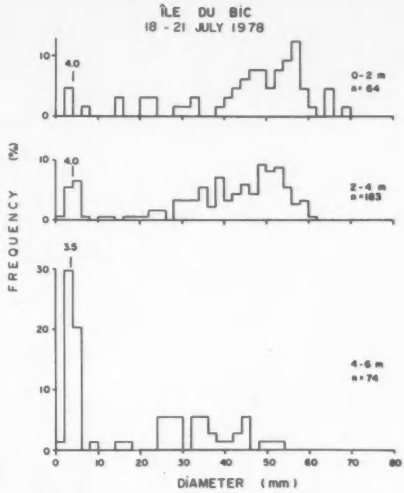

FIG. 11. Size–frequency distributions for urchins at different depths at Île du Bic.

group at 7–10 mm diameter. As at Godbout and Anse Saint-Pancrace, the relative frequency of individuals between 14 and 50 mm in diameter at Les Îlets and Baie Mitis was low and relatively even.

At Île du Bic (Fig. 11) the population resembled that at Anse aux Basques on the north shore. There was a cohort of small individuals at 3.5–4.0 mm test diameter, which was very weakly represented at 0–2 m deep but increasingly prominent at greater depths, and a broad group of large urchins suggesting an accumulation of year-classes.

At Rocher de Cacouna (Fig. 12) the population structure was strikingly similar to that at Port-au-Saumon on the opposite side of the estuary, there being a cohort of small individuals, no individuals of intermediate size, and a predominant broad group of urchins larger than 42 mm in diameter.

In summary, urchin populations in the outer portion of the Saint Lawrence Estuary were characterized by high frequencies of small urchins, representing one to several cohorts, and low frequencies of larger urchins (Fig. 13). In the inner portion of the Lower Estuary, although small urchins were rare or absent above 2 m in depth, at greater depths one or two very well-defined cohorts of small urchins were present. In contrast to the low frequencies of medium-sized and large urchins in the outer portion of the estuary, in the inner portion of the Lower Estuary there was a gradual increase in the frequency of individuals above 16 mm test diameter. This suggests that here longevity is increased and the broad group of larger urchins probably represents an accumulation of year-classes. In the Upper Estuary, although urchins were present in low numbers and entirely absent above 2 m in depth, the populations were unusual in that they were bimodal. There was a cohort of small urchins, no individuals of intermediate size, and then a broad group of very large individuals. Here it would appear that whereas recruitment

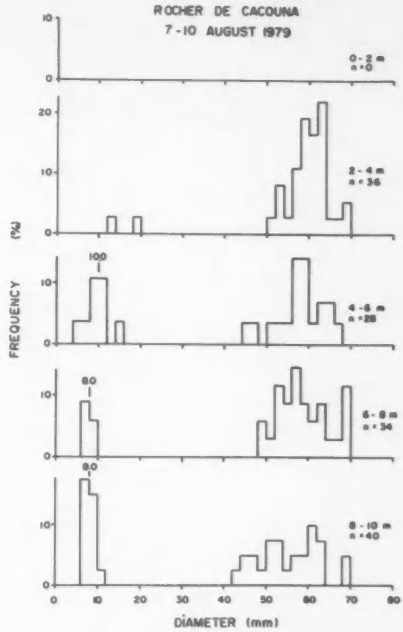

FIG. 12. Size–frequency distributions for urchins at different depths at Rocher de Cacouna.

and early survival are low, once urchins reach 40–50 mm in diameter, longevity is very high.

CHANGES OVER TIME AT POINTE MITIS AND ANSE AUX BASQUES

In June 1978 at Pointe Mitis, a very high density of small urchins was found on a relatively flat cobble and pebble bottom. Each sample (0.25 m^2) taken contained between 139 and 457 urchins and showed the presence of two distinct groups, one at 2–3 mm in test diameter and another at 8–9 mm in test diameter. We thought that these groups probably represented successive year-classes, because *S. droebachiensis* has been reported to increase in test diameter by 5–10 mm annually (Miller and Mann 1973; Lang and Mann 1976; Swan 1958). We took additional samples here to follow the growth of these cohorts. Figure 14 shows size–frequency distributions for samples taken from Pointe Mitis from 1.5 to 2.1 m deep on seven dates between June 1978 and May 1981. The two cohorts remained well defined throughout this period, but showed remarkably little growth. During the 3-yr period the mean size of the first group advanced by only 3.5 mm, and there was little change in the position of the second group.

In the estuary, *S. droebachiensis* spawns during June (Jalbert et al. 1982). The duration of its pelagic larval phase varies from 7 to 22 wk (Strathmann 1978). The first well-defined group of small urchins at Pointe Mitis, at 2.2 mm in

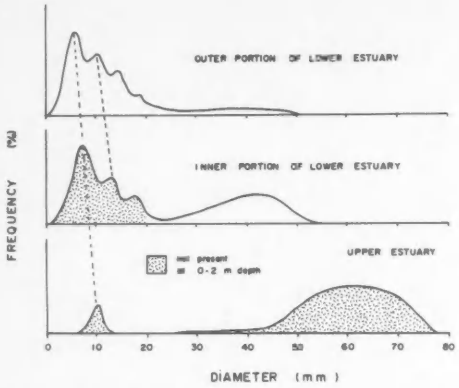

FIG. 13. Summary of changes in the size–frequency distributions for urchins going from the outer portion of the Lower Estuary to the Upper Estuary.

June 1978, probably represents individuals recruited from the spawning in 1977. The second group may have been produced by a heavy recruitment 1 or 2 yr earlier, or alternatively it could be an accumulation of year-classes. This latter is more probable considering that it remained in about the same position from 1978 to 1981 and is supported by the fusion of the first group with the second during our period of observation. There was no evidence of new individuals entering the population at Pointe Mitis during 1978–81 (Fig. 14).

Repetitive sampling was also made at Anse aux Basques, at the interior of the cove (Himmelman et al. 1983a). Between July 1978 and July 1980 the population size-structure showed little change, except for the slow growth of the first cohort of small urchins by about 3 mm. The exact position of this cohort in July 1978 varied from 4.3 mm in shallow water to 2.6 mm at greater depths, and it also probably represents recruitment from 1977. At Anse aux Basques there was also no evidence of new recruitment. Thus, our observations over a 2- to 3-yr period at Pointe Mitis and Anse aux Basques clearly showed that the growth rate of juveniles was markedly less than that reported for *S. droebachiensis* in the literature.

Relative Growth Rate in the Different Regions of the Estuary

The first well-defined group of small urchins, observed in each of the different transects on the north and south coasts of the estuary, probably corresponds with the first group of small urchins seen at Pointe Mitis and Anse aux Basques and represents the same successful recruitment pulse assumed to occur in 1977. If so, the mean size of this group reflects the growth rate in the various regions. On the north shore at Anse Saint-Pancrace, in the outer portion of the estuary, this cohort was at 3 mm test diameter in August 1978 (Fig. 5), whereas at the same time at Anse aux Basques, in the inner portion of the Lower Estuary, it was at about 4 mm test diameter (Fig. 6, 7). In the Upper Estuary at Port-au-Saumon, the mode was at about 5.5 mm (Fig. 8). Thus, the increase in size of this

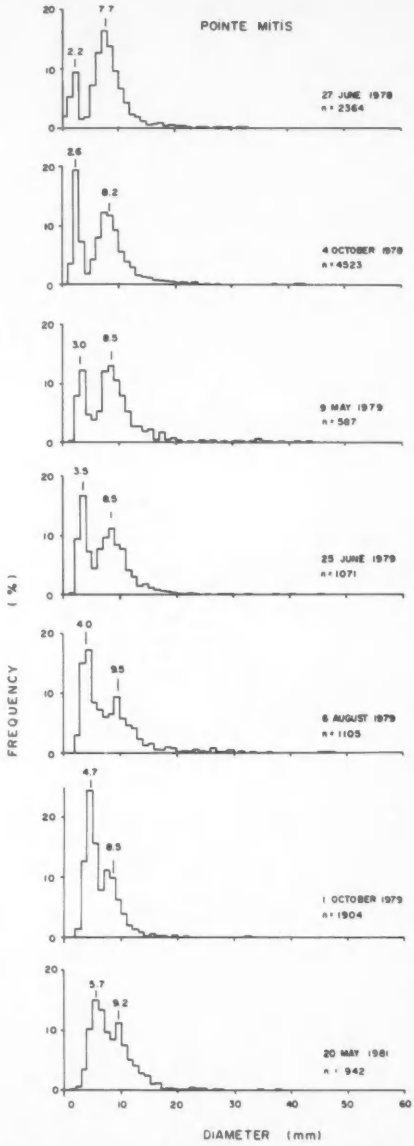

FIG. 14. Size–frequency distributions for urchins sampled at 1.5–2.1 m in depth at Pointe Mitis for seven different dates between June 1978 and May 1981.

well-defined recruitment pulse, going from Anse Saint-Pancrace to Port-au-Saumon, suggests a progressive increase in the growth rate of urchins. At Godbout in June of the following year the first cohort was at 5.3 mm test diameter

TABLE 1. Mean annual salinity (‰) (± SD) and annual minimum and maximum salinities at different depths for a region 15 km east and west and north and south of each of the locations where quantitative samples of urchin populations were collected. Data from Marine Environmental Data Service (MEDS), Government of Canada, Ottawa.

Depth (m)	‰salinity $\bar{x}$	SD	(min.−max.)	(*n*)	Depth (m)	‰salinity $\bar{x}$	SD	(min.−max.)	(*n*)
	Godbout					*Les Îlets*			
0−4	28.9	1.25	(24.2−31.7)	(51)	0−4	27.7	1.10	(23.1−29.1)	(76)
5−11	29.4	1.25	(24.2−31.7)	(56)	5−11	28.6	1.06	(25.4−29.9)	(75)
12−20	30.0	0.80	(26.5−31.0)	(31)	12−20	29.5	0.51	(28.1−31.0)	(40)
	Anse Saint-Pancrace					*Baie Mitis and Pointe Mitis*			
0−4	24.9	2.03	(20.6−28.2)	(11)	0−4	26.4	1.51	(24.9−28.3)	(5)
5−11	28.8	1.28	(26.0−29.8)	(7)	5−11	27.1	1.54	(24.9−28.9)	(10)
12−20	29.1	0.01	(29.1−29.1)	(2)	12−20	29.0	0.79	(27.6−29.7)	(6)
	Anse aux Basques					*Île du Bic*			
0−4	25.1	4.40	(12.2−30.1)	(185)	0−4	25.6	4.75	(13.0−30.7)	(60)
5−11	26.1	4.78	(14.8−31.3)	(159)	5−11	26.5	4.31	(13.9−30.1)	(66)
12−20	28.6	1.25	(25.7−31.1)	(72)	12−20	28.4	1.66	(24.4−30.8)	(25)
	Port-au-Saumon					*Rocher de Cacouna*			
0−4	18.8	2.96	(12.8−27.0)	(180)	0−4	23.6	2.76	(12.7−31.8)	(262)
5−11	22.1	3.06	(13.8−28.6)	(169)	5−11	25.3	3.09	(13.4−32.1)	(238)
12−20	24.6	3.61	(16.4−30.0)	(157)	12−20	27.0	2.90	(18.9−32.7)	(160)

in shallow water (Fig. 4), about 2 mm larger than at Anse Saint-Pancrace in 1978 (Fig. 5).

A similar pattern was seen along the south shore of the estuary. The relative position of the first cohort of urchins, probably representing recruitment from 1977, suggests that growth was least at Pointe Mitis, Baie Mitis, and Les Îlets in the outer portion of the Lower Estuary; intermediate at Île du Bic in the inner portion of the Lower Estuary; and greatest at Rocher de Cacouna in the Upper Estuary (Fig. 9, 10, 11, 12, 14).

Succeeding year-classes are generally not well defined; however, a second cohort is suggested by the data for a number of transects and its relative position in the various locations supports the trends in growth rate suggested by the position of the first mode. One final indication that the growth rate increases going up the estuary is the increase in the maximum size reached at the different sites going up the estuary (Fig. 4−13).

RELATION BETWEEN CHANGES IN URCHIN POPULATIONS AND THE ESTUARINE GRADIENT

Sea urchins and other echinoderms are particularly sensitive to departures from normal oceanic salinities. Thus changes in the urchin populations at the various levels along the Saint Lawrence Estuary (as summarized in Fig. 13) may be related to the transition from saline to nonsaline conditions. A list of annual mean salinities and extremes for three depth intervals in the region of each of the transects is presented in Table 1. Most of the observations were made during June through September.

In the outer portion of the Lower Estuary, at Godbout and Anse Saint-Pancrace on the north coast, and at Les Îlets, Baie Mitis, and Pointe Mitis on the south coast, the mean annual salinity was high (25‰ or greater). Here, urchin densities were very high, especially in shallow water (Fig. 4, 5, 9, 10, 14). The abundance of small urchins indicates that the recruitment rate was high.

In the inner portion of the Lower Estuary at Anse aux Basques and Île du Bic, although the mean annual salinity was similar to that in the outer portion of the Lower Estuary, the variance was greater and the minimum values were much lower (Table 1). At 0−2 m in depth at Anse aux Basques and Île du Bic, urchins were mainly large and medium-sized; small urchins were rare (Fig. 6, 7, 11). With increasing depth, the numbers of small urchins increased sharply and became comparable to those in the outer portion of the Lower Estuary. We hypothesized that small urchins, having a large surface area to volume ratio, would be more sensitive to reduced salinities than larger animals, and this was recently confirmed in the laboratory (Vigneault, Drouin, Guderley, and Himmelman, unpublished data). For example, when different size groups were placed in seawater diluted to 8‰ for 24 h and then returned to normal seawater, there was 50% mortality for urchins measuring 10−15 mm in test diameter (n = 10), but no mortality for animals measuring 30−35 and 50−60 mm in diameter. The population size-structures suggest there are periodic drops in the salinity of surface waters at Anse aux Basques and Île du Bic that are lethal to small individuals.

Salinities were low in the Upper Estuary. Although at Port-au-Saumon at 0−4 m deep the mean annual salinity was

18.8‰, Marine Environmental Data Service (MEDS) data show that the mean monthly salinity was 16.6 ± 1.97 (n = 65) in June and 16.2 ± 1.74 (n = 21) for October. At 5−11 m deep the mean monthly salinity was 20.6 ± 3.25 (n = 55) in June and 18.9 ± 2.51 (n = 18) in October. The mean annual salinities at Rocher de Cacouna were not appreciably lower than in the Lower Estuary, but MEDS data show that periods of reduced salinities can occur. The mean during May was 18.2 ± 0.59‰ (n = 11) at 0−4 m deep, 19.3 ± 0.56‰ (n = 22) at 5−11 m deep, and 20.0 ± 0.86‰ (n = 13) at 12−20 m deep. There were marked differences in the size−structure of the urchin populations at Port-au-Saumon and Rocher de Cacouna (Fig. 8, 12), compared to the populations in the Lower Estuary, corresponding to the decrease in salinity. No urchins were found in shallow water (0−2 m deep), and at greater depths there was a low density of small and large urchins and no medium-sized individuals. The absence of urchins above 2 m in depth and the low recruitment rate are probably caused by low salinities. The rarity of intermediate-sized urchins suggests that urchins are often killed before they reach a size where they are less sensitive to salinity reductions. One 18-mm urchin was found in the lower part of the transect at Port-au-Saumon (at 15 m in depth, Fig. 8). Some juveniles probably survive in deeper water through the intermediate-size range; then, after reaching a size which is more tolerant of decreased salinities, they can move to shallower water. At Port-au-Saumon, urchins larger than 50 mm in diameter can evidently tolerate mean salinities of 16−17‰ during June and October, and at Rocher de Cacouna urchins larger than 45 mm in diameter can withstand a mean salinity of 18‰ during June. The accumulation of large individuals in these populations indicates that longevity is great after a diameter of 40−50 mm is reached.

Thus, urchin populations show changes which appear to be related to the salinity gradient of the Saint Lawrence Estuary. In the outer portion of the Lower Estuary, there is a high rate of recruitment and no indication of periodic mortalities. In the inner portion of the Lower Estuary, periodic drops in surface salinities might account for the lack of small urchins above 2 m deep. Recruitment is high just below 2 m deep where salinity is more stable. The Upper Estuary is a marginal habitat for urchins. They cannot survive above 2 m in depth, and below 2 m deep recruitment and survival of small individuals is low. Tolerance to reduced salinities is increased after a size of 40−50 mm in test diameter is reached.

Relations Among Urchin Grazing, Algal Production, and Urchin Growth

An increase in the growth rate of urchins at various locations going up the estuary was indicated both by the general increase in the size of individuals, and by the progressive increase in the mean size of the 1977 cohort. This cannot be explained by reduced salinity along the estuarine gradient. However, food conditions strongly affect the growth rate of urchins (Keats et al. 1983; Larson et al. 1980; Vadas 1968, 1977) and differences in food availability could explain differences in urchin growth rates in different regions of the estuary.

In the Lower Estuary, rocky areas support high densities of urchins, and macrophytes other than coralline algae are scarce. The low algal abundance is caused by severe urchin grazing. When abundant urchins were removed from an experimental barren area at Anse aux Basques, an *Alaria* bed developed between 0 and 2 m in depth within a 3- to 4-mo period, and extended to 6 m in depth after a 2-yr period (Himmelman et al. 1983). Only a small number of algal species, including *Agarum cribrosum*, *Ptilota serrata*, *Phycodrys rubens*, *Kallymenia schmitti*, and encrusting coralline algae, are normally found among dense urchin populations. These species appear to be unattractive foods for urchins, as they are not heavily grazed upon. Also, laboratory studies have shown that urchins have a very low preference for *Agarum* and *Ptilota* (Himmelman 1969, 1980) and when urchins are kept on a diet of *Agarum*, *Ptilota*, or coralline algae, somatic and gonadal growth is poor (Keats et al. 1983; Larson et al. 1980; Vadas 1968). Favorable algal foods for urchins, such as *Laminaria* and *Alaria*, are found almost exclusively in shallow water. Observations made in Newfoundland indicate that the size of the subtidal algal fringe is determined by the interaction between urchin grazing and wave activity (Himmelman 1969, 1980). During the winter in exposed locations where an *Alaria* fringe is normally present, the *Alaria* zone expands to greater depths. In more protected locations where *Alaria* is not found during the summer and autumn, *Alaria* appears in shallow water during the winter. The expansion of the *Alaria* zone during winter is favored by low consumption rates of the urchins, and by strong wave activity which keeps algal fronds in movement and makes them less accessible to urchin attacks. In spring, the consumption rate of the urchins increases and during calm periods in the summer they move upward to graze on the *Alaria*. This results in a recession of the subtidal *Alaria* fringe.

The algae in the urchin-dominated communities in the outer portion of the Lower Estuary, particularly those preferred by urchins, are in very short supply. Here low growth rates were observed. Larger urchins, which actively move about searching for food, were concentrated in shallow water close to the major zone of algal production. Often their grazing has greatly reduced or eliminated the infralittoral algal fringe.

In the inner portion of the Lower Estuary, algal production in shallow water is greater and *Laminaria* beds may be present (Lavergne and Himmelman 1983). Drift algae are often present and even areas supporting dense urchin populations, where *Laminaria* and other favorable food species cannot become established, are supplied with algal debris. In contrast with the transect sites in the outer portion of the Lower Estuary, at Anse aux Basques in the inner portion of the Lower Estuary, there was no marked change in the abundance of medium-sized and large urchins with depth. This could reflect the greater availability of food. We have observed that drift algae, particularly pieces of *Laminaria longicruris*, are frequently present in the vicinity of Anse aux Basques. The inner portion of the Lower Estuary supports an increased growth rate, as indicated by the slightly increased size of the 1977 cohort, and the generally larger size of individuals.

In the Upper Estuary, the urchin density is very low and urchin grazing must have only a slight effect on algal populations. Here there was a dense algal zone with *Laminaria*

spp. and foliose red algae to a depth of 2–3 m. The high turbidity at this level in the estuary, and consequent low light penetration, probably accounts for the absence of fleshy algae and rapid decrease in coralline algae at greater depths. The abundance of favorable algal foods, particularly in relation to the low urchin numbers, is probably responsible for the accelerated growth rate of urchins in this region. Food availability is thus probably the major factor controlling the growth rate of urchins in the Saint Lawrence Estuary.

Considerations for an Urchin Fishery

Although urchins are indeed abundant in the Saint Lawrence Estuary, their suitability for an urchin roe industry varies considerably in the different geographical regions of the estuary. In the Lower Estuary, the large numbers of individuals of the 1977 cohort indicates that in years when conditions are favorable for the development of urchin larvae, recruitment is extremely successful. However, because of the high rates of recruitment and juvenile survival, densities become extremely high, $250-400 \cdot m^{-2}$, and the resultant grazing pressure severely limits algal production. Therefore, in most locations there are high densities of mostly small individuals. Harvesting such populations would theoretically reduce grazing and permit greater algal production. Indeed, in the experimental situation at Anse aux Basques where the numbers of urchins were drastically reduced, there was a marked acceleration in the growth rate of the remaining urchins (Himmelman et al. 1983a). However, the level of harvesting would have to be extremely high, and would have to include intermediate-sized animals to have a significant effect. This would be economically impractical.

By contrast, in the Upper Estuary most urchins are large being 5–7 cm in diameter. However, the abundance of urchins is very low and in most locations the cost of harvesting the urchins would be prohibitive. Furthermore, recruitment in the Upper Estuary is feeble and only a low recovery rate of harvested populations would be expected.

The region with the commercially most useful populations of urchins is near the boundary of the Lower and Upper Estuaries. In a qualitative survey made over a large area of the Estuary (Lavergne and Himmelman 1983), two such populations were found. One was in the region of Bic on the south shore, and the other at Cap de Bon Désir, 6 km southwest of Anse aux Basques on the north shore (Fig. 1). Here large urchins were abundant, and these populations were adjacent to an abundant supply of *Laminaria* so that gonadal production would probably be high. However, the areas supporting these populations were not large and could easily be depleted. Further, we noted that small urchins were not abundant at these sites, perhaps because of salinity problems or possibly due to the higher rate of sedimentation in these areas. Therefore, here also the recovery rate may be low.

At a number of locations in the Lower Estuary there are specific conditions which have led to populations of large urchins probably having elevated gonadal production. One situation is subtidal areas where the numbers of urchins have been markedly reduced by ice action during the winters. In such areas there is a rapid growth of algae during the spring and summer providing food for the remaining urchins, located in depressions or in adjacent areas. This situation is most common on the south shore of the estuary, where ice action is greatest (Lavergne and Himmelman 1983). *Laminaria* and large urchins are also often found in locations where there are boulders or rock outcrops surrounded by sand. The abrasive action of the sand during storms apparently reduces the urchin numbers and permits the growth of algae.

The sporadic recruitment of urchins in the Saint Lawrence Estuary is not a particular response to estuarine conditions, as it has also been observed for *S. droebachiensis* in Newfoundland (Himmelman 1969) and Nova Scotia (W. G. Wharton, Dalhousie University) and for other echinoids (Buchanan 1979). The factors determining whether recruitment is successful are unknown.

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An Echo Counting and Logging System (ECOLOG) for Demersal Fish Size Distributions and Densities

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Target strength of fish is dependent on their size, behavior, and density, and uncertainties about these parameters under field conditions affect the interpretation of acoustic survey data. The echo counting and logging system, ECOLOG, appears to offer information on these important parameters. The dual-beam system is described and results of a test cruise are analyzed. Published data on the relation of target strength to fish size are used to generate an "acoustic size-composition" from otter-trawl catches. Correspondence between the converted otter-trawl samples and acoustic data suggest that the system is generating direct information on demersal fish size and density and may thus be useful in verifying the results of echo sounder surveys. Main components of variation among samples and between sampling methods are ascribable to small-scale spatial heterogeneity of size distributions, although day–night behavior differences contribute significantly to the total heterogeneity.

DICKIE, L. M., R. G. DOWD, AND P. R. BOUDREAU. 1983. An echo counting and logging system (ECOLOG) for demersal fish size distributions and densities. Can. J. Fish. Aquat. Sci. 40: 487–498.

L'intensité des échos produits par les poissons dépend de leur taille, de leur comportement et de leur densité, et, dans les conditions qui prévalent sur le terrain, ces paramètres influencent l'interprétation des données de relevés acoustiques. Le système de comptage et d'enregistrement d'échos, l'ECOLOG, semble fournir une information sur ces paramètres importants. Nous décrivons dans le présent article le système à double faisceau et analysons les résultats d'une croisière d'essai. À l'aide de données publiées sur la relation entre l'intensité des échos et la taille des poissons, nous avons obtenu une « composition par taille acoustique » des prises de chalut. La correspondance entre les échantillons de chalut convertis et les données acoustiques donne à penser que le système fournit une information directe sur la taille et la densité des poissons démersaux. Il peut donc servir à vérifier les resultats des relevés par écho-sondeurs. Les principaux éléments de variation entre échantillons et entre méthodes d'échantillonnage peuvent être imputés à une hétérogénéité spatiale à petite échelle des distributions de taille, bien que des différences de comportement diurne et nocturne contribuent de façon significative à l'hétérogénéité totale.

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ACOUSTIC surveys have for many years been recognized as potentially the most direct and efficient means of estimating abundance of fish. There have been developmental problems, for example, difficulties with intership calibration and apparent variations among species and fish sizes. However, the general validity of the method is increasingly supported by evidence of acoustic indices of change in distribution and abundance being related to changes in total landings. Serious uncertainties remain which limit the ability to refine these relative abundance and distribution data in the direction of density information relevant to catch rates and absolute abundance levels. Three missing parameter values are important to such improvement. These are (1) the relation of target strength to fish size under natural conditions, (2) the relation of target strength to fish density within the sonified cone, and (3) the relation of sample distances and volumes to estimates of population density in the presence of schooling or other local aggregation phenomena.

The fish echo counting and logging survey system (ECOLOG) developed by the Marine Ecology Laboratory of the Bedford Institute of Oceanography appears to offer numerical field information on these parameters. This paper describes ECOLOG and some test results derived during two short experimental cruises. The dual-beam system permits interpretation of the acoustic signals from individual fish. Data have been derived from Atlantic cod (*Gadus morhua*),

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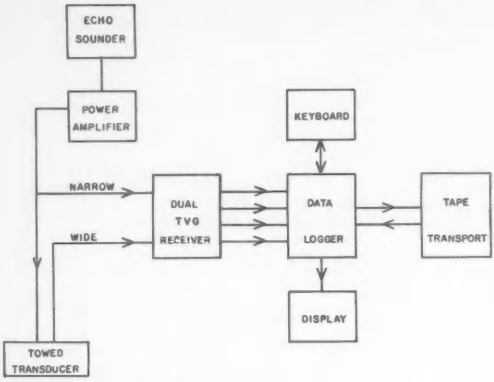

FIG. 1. Block diagram of ECOLOG.

haddock (*Melanogrammus aeglefinus*), and pollock (*Pollachius virens*) in various concentrations and degrees of mixture. The target strength–fish size relationship which best matches the acoustic data to the size-compositions of the trawl catches is very close to what has been derived in published laboratory-type measurement experiments, and is apparently unaffected by densities commonly encountered among these various demersal species. However, estimates of average size and density are sensitive to normal variations in local density and behavior. This confirmation of what have previously been assumptions about the effects of fish population behavior on acoustical data should promote the development of fisheries population parameters through acoustic surveys, at the same time opening up the possibility of further study of fish population microstructure and behavior in relation to abundance.

The Instrument System, Data Collection, and Interpretation

ECOLOG (Fig. 1) is an acoustic data-logging system which uses a towed dual-beam transducer to sample and record echoes from a vertical cone of sonification. The entire water column below the transducer is sampled at a rate of once per 100 microseconds. Echoes from each transducer are amplified by a special dual time-varied gain receiver, then digitized, reformatted, and, along with time after transmit, stored on digital magnetic tape for later analysis.

System Components and Specifications

(a) The towing system — The transducer, a dual-beam unit, model SP268LT, constructed by Ametek Straza and based on the theoretical developments of Ehrenburg (1974) is housed in a 1.4-m dead weight towed body designed by Fathom Oceanology. The transducer contains two independent, aligned transducers with beam angles, at the $\frac{1}{2}$ power points, of 26° (wide) and 6.5° (narrow). The towed body is suspended over the side of the survey ship from a hydraulic crane and connected through a slip ring assembly to the ship's laboratory by a 150-m 4-conductor towing cable.

(b) The analog system — The analog system consists of an Instruments Inc. 5-kW model SPG-4 power amplifier operating at a frequency of 50 kHz and a pulse length of 0.4 ms. The transmission rate, which is obtained from the ship's Simrad EK50 echosounder, is 96 pulses per minute. The transmitter is connected to the narrow transducer. Echoes from the two transducers are received on a special dual time-varied gain (TVG) receiver which is designed to accept signals from two transducers having different sensitivities. It consists of two fixed-gain preamplifiers, and two receivers with base gains adjusted to compensate for transducer sensitivity differences, with subsequent gains controlled by a single digital TVG having an accuracy within ±0.5 dB at 100 m and a range of 10–400 m. The 50-kHz signals are demodulated and, along with the transmit and bottom-generated pulses, are made available at the front panel for monitoring and recording.

(c) The data logging system — This unit is a microprocessor-based data acquisition system designed to sample the demodulated echo signals at 100-μs intervals for amplitude and time-after-transmit. The unit consists of a special interface board, an Intel 80/05 single board microcomputer, an Intel common RAM board, an Intel 80/30 single board microcomputer, a Burroughs Self-Scan display, decwriter IV and Pertec 9 track, 800 B.P.I., tape transport. These standard products are hard-wired and programmed for this particular application.

The analog-demodulated signals from each transducer are digitized by a 12-bit ADC. For each 100-μs sample, if the narrow beam signal is above the predetermined threshold of a 0.7-V peak, 6 bytes of data are stored, bytes 1 and 2 for time after transmit, 3 and 4 for the wide beam, and 5 and 6 for the narrow beam. On the 80/30 microcomputer these data are reformatted and along with date and time of day are transferred to the Pertec tape transport in buffers of ~12K bytes. The Burroughs Self-Scan displays the current time, status, depth, and echo count for each transmission. Initialization and termination of data logging are controlled from a decwriter IV through single character commands. The tape transport is a "read after write" unit which verifies that the data recorded are in the correct format. Routines are available which permit the operator to check the data recorded following a run.

The Dual-Beam Transducer

Traynor and Ehrenberg (1979) show that two precisely aligned transducers of different beam angles can be used to correct the effect of beam directivity on target strength. This correction depends on the fact that the received signals fall off from the axis of the sound cone faster for the narrow beam than for the wide beam. The ratios of the transducers' diameters can be chosen such that within the half-power points on the narrow, an echo level (i.e. in dB) returned to the two transducers will have a constant ratio independent of distance off the acoustic axis. If the sensitivities of the transducers are held constant, the ratio of the two echos can be used to estimate the target strength of an object.

It is clear that with such a system the relative sensitivities of the two transducers, their precise alignment, and transmit

TABLE 1. Results of "Light Bulb" experiment. Volts RMS received is given for both transducers as well as a calculated target strength value for each station. Received voltages: *A*, 1 V; *B*, 5 V.

Distance off axis (cm)	Volts RMS wide	Volts RMS narrow	Target strength (dB)	Standard deviation
		A		
0	1.05	1.02	−40.98	1.28
20	0.75	0.79	−44.62	2.22
40	0.91	0.87	−42.02	1.07
50	0.83	0.79	−42.81	1.26
60	0.77	0.71	−43.05	1.29
70	0.71	0.61	−43.38	1.17
80	0.76	0.59	−41.74	0.95
90	0.66	0.49	−42.48	0.78
100	0.64	0.41	−41.51	1.23
			−42.58±0.078	1.73
		B		
0	3.92	3.91	−44.17	2.26
20	4.35	4.46	−43.49	2.10
40	3.73	3.84	−44.74	1.50
50	3.96	3.94	−44.16	2.60
60	4.70	4.37	−41.80	1.32
70	3.85	3.46	−43.36	2.05
80	3.28	2.82	−44.22	1.27
90	3.01	2.41	−44.36	1.00
100	2.81	2.02	−43.95	0.84
110	2.58	1.65	−43.78	1.43
120	2.21	1.24	−43.85	0.75
130	1.95	0.91	−43.46	0.95
140	1.68	0.65	−43.13	0.97
			−43.71±0.064	1.71

responses are critical to interpretation. We have used the services of an acoustic calibration barge maintained by the Defence Research Establishment — Atlantic to check the accuracy of our transducer alignments and sensitivities and to carry out appropriate calibrations. Figure 2 shows the polar plots of the two transducers. The receive sensitivities were recorded at -180.4 dB V^{-1} μPa^{-1} (narrow beam) and -192.8 dB V^{-1} μPa^{-1} (wide beam). The source level was $+226.7$ dB V^{-1} μPa^{-1} at 1 m.

To illustrate the functioning of the system we present in Table 1 the results of a simple experiment in which a 100-W light bulb with a diameter of 66 mm was insonified at different positions in the dual beam. The bulb was aligned with the transducers at 8 m in depth, with the bulb placed 14 m away. The bulb was then sonified on axis and at successive short distances from axis until the echoes went below threshold. Two hundred transmissions were recorded at 1, 3, and 5 V at each station. In the table selected analogue results converted to volts root mean square (RMS) are shown for each station. Average target strength, calculated as (40 log volts RMS_{wide} − 20 log volts RMS_{narrow}) + K, and its standard deviation are also given for each station; K being the summation of calibration factors. The theoretical expectations of the system are met to within about 5%. Such low standard deviations throughout indicate satisfactorily low noise levels.

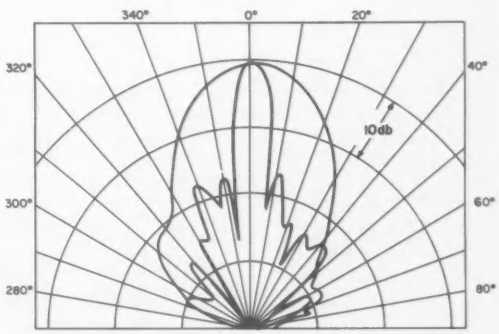

FIG. 2. Polar plots of the dual-beam transducer.

DATA COLLECTION

The data analyzed in this paper were collected on two short experimental cruises carried out during October 1980 and February 1981 to the south and east of Brown's Bank on the Scotian Shelf (near 42°40′N lat. 63°30′W long.).

Preliminary explorations of the chosen area were made

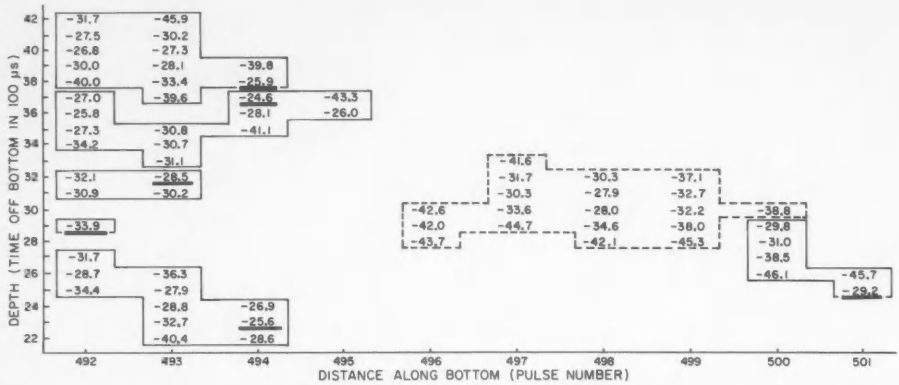

FIG. 3. A two-dimensional array of target strengths calculated from the dual-beam transducer signals and arranged to show the grouping with depth (time off bottom) and distance along bottom (successive pulses). The signal groupings outlined in solid line correspond with our definition of single fish, the group outlined by a broken line is defined as a multiple. The peak target strength used to index size in each group is underlined.

using the ship's hull transducer in transects run at full cruising speed. When a region of suitable fish concentrations on relatively flat and satisfactory otter-trawling bottom was found, the transducer was lowered over the side and a pattern of replicate transects was run, usually at about 4 m/s (8 knots). Periodically the transducer was shipped and replicated 30-min hauls were made with a Yankee-36 otter trawl fitted with a $\frac{1}{4}$-in. (6.35 mm) mesh liner in the cod end. Koeller (1981) describes the construction of this trawl.

During both cruises acoustic runs were made during different times of the day and night but otter-trawl tows were confined to the daylight hours. During the first cruise, an area was chosen in different parts of which there seemed to be persistently different degrees of mixture of the three principal demersal species: haddock, cod, and pollock. Appropriate details are given in connection with the analysis. Completely symmetrical statistical designs for the acoustic transects and tow patterns were frustrated by the influence of bad weather, occupation of intended tow paths by commercial fishermen, fouling of gear on patches of rough bottom, and by the occasional appearance of massive schools of squid. The second cruise was on smooth hard-sand bottom where a stable high concentration of fish appeared to be overwhelmingly dominated by a restricted size-range of haddock. Some interference was accountable to commercial fishing gear and weather.

In both areas the water depth averaged about 100 m and the transducer was towed at a speed of 3.5–4 m/s (7–8 knots) at a depth of about 25 m below the surface. On the second cruise repeat transects were run with the transducer held at a number of different depths above bottom and different speeds in an effort to collect information on possible coincidence counting of fish.

In general, acoustic transects were ~11 km in length and were sampled in a regular sequence during day and night as long as conditions permitted. Otter-trawl tows were of 30-min duration during daylight over a previously specified section of the acoustic transect. During the second cruise this objective was assisted by the use of a Loran-C navigation system although the continued presence of variable crosswinds, tidal and wind currents made high precision in the transects impracticable.

SIGNAL INTERPRETATION AND COMPILATION

The data tapes returned to the laboratory are converted from the 8-bit word permitted by the shipboard microprocessor to the 60-bit word employed by the CDC computer we use for analysis. At this time, data concerning the date and time of the acoustic runs are read from the tape. For each interrupt a line of data is dumped to disc for storage and later analysis. This line of data includes buffer number, time (in hundreds of microseconds) from transducer to interrupt, time from transducer to bottom, A/D (in bits) received on the wide transducer, A/D received on the narrow transducer, and a pulse number. Pulse numbers are incremented from the start of each run. With these data we reconstruct a matrix of interrupts with pulse number (distance) being the horizontal axis and time of interrupt (depth) forming the vertical axis.

Perhaps the most critical part of the signal-interpretation procedure is the classification of the signal data according to a predefined definition of "single fish" or "multiple echoes." As is well recognized, transmission rates, ship's speed, beam angles, and water depths of the order specified here will result in detection of a stationary object near bottom in as many as four successive pulses depending on its position relative to the centre of the path of movement of the sonified cone (MacNeill 1971). Furthermore, at the sampling rate of 100 μs and a pulse length of 0.4 ms, we obtain signal measurements at vertical intervals of 7.5 cm. A large fish, at the axis of the beam, may yield a signal with a peak voltage of 10 V with an envelope up to 600 μs.

Taking these factors into account we divide our matrix of interrupts into aggregations of interrupts which we define as separate targets in the water column. Adjacent interrupts in both directions are grouped together unless the amplitude of the interrupts has peaked, fallen, and peaked again along

TABLE 2. Comparison of wide and narrow beam transducers as they define the pulse envelope. Average volts peak ($\bar{x}$) along with standard deviations (SD) are given for each interrupt in the envelope.

Number of interrupts in envelope	Transducer		Interrupt number 1	2	3	4
1	Wide	$\bar{x}$	0.95			
		SD	0.023			
	Narrow	$\bar{x}$	0.90			
		SD	0.013			
2	Wide	$\bar{x}$	0.94	1.00		
		SD	0.022	0.017		
	Narrow	$\bar{x}$	0.89	0.97		
		SD	0.012	0.009		
3	Wide	$\bar{x}$	0.93	1.00	0.97	
		SD	0.021	0.018	0.019	
	Narrow	$\bar{x}$	0.88	0.96	0.99	
		SD	0.014	0.009	0.008	
4	Wide	$\bar{x}$	0.94	1.01	0.98	0.98
		SD	0.024	0.019	0.021	0.018
	Narrow	$\bar{x}$	0.89	0.97	0.99	0.98
		SD	0.015	0.008	0.007	0.007

either axis. In such a case the two peaks are defined as two separate targets. Arrays of interrupts which are less than three interrupts long are defined as belonging to one target. This method of analysis thus permits identification of peak voltages in the data. Once this grouping process has been completed the data are classified as representing single fish if the group has been observed in less than five successive pulses. All groups which have been observed in five or more pulses are classified as "multiples" and are excluded from further analysis. We have not yet attempted to deal further with the precise shapes or volumes under the peaks.

Figure 3 is a visual representation of a section of an aggregation of edited acoustic data, obtained on the February 1981 cruise. We have encircled in the set all the groups of numbers in the array which fit our criterion of single fish and marked the peak voltage used to index its size. The sequence was chosen deliberately to illustrate a group (circled in broken line) of interrupts which does not conform to the definition of a "single" and which was classified as a "multiple." At each analytic run of acoustic data our programs are designed to give a count of interrupts classed as single fish and of number of interrupts rejected as multiple. In the data obtained on the cruises multiples constituted as much as 30% of the total number of interrupts in some runs, with an average of about 15%.

Once the entire array of data corresponding to a selected transect has been classified, the single fish groups are reviewed and the peak voltage is identified for each group on both the wide and narrow transducers. Because it is impossible to obtain absolutely identical pulse envelopes in the two transducers, there is a risk that some of the difference in peak level of the signal might be due to the relative positions of the peaked samples within the pulse. To check this possibility we have obtained a series of simultaneous hydrophone inputs of different signal strength and pulse lengths from the two transducers. A small sample of the data (Table 2) shows that even in signal envelopes narrow enough to contain only one sample, the peaks vary by less than ±5% in amplitude, whereas in groups giving two or more samples the variation is less than ±3%. Variations in the height of peaks small enough to contain only a single sample show wider variation because of the small differences in rise time from the two transducers.

The problem of acoustic noise is important in the interpretation of fish echo data. Some signals are generated by small organisms or other objects in the water, about which we have relatively little information. In addition there are extraneous noises, some of them generated by the survey ship, the towing cables, as well as other sources. These are largely eliminated by our threshold of 0.7-V peak. After a study of samples of the data we have imposed two other editing restrictions on the data to be included in the information series. First, if in any instance a signal reaches a peak voltage on the narrow transducer which is higher than the peak voltage on the wide transducer, both signals are rejected as noise. In theory a target exactly on the axis of the sonified cone should give an equal signal on both transducers. Otherwise, the signal strength should be smaller on the narrow transducer. Sampling of the two should reflect this difference within limits of error of coincidence of the signal pulse envelopes. In practice we found that when the narrow beam amplitude was larger it was, with few exceptions, very much larger. We have therefore not concerned ourselves with incorporating the permissible statistical latitude in the actual editing operation.

Second, a noise problem was held to be indicated in all cases where the signal strength of the interrupt exceeded that of our maximum recordable fish-echo strength of a 10-V peak.

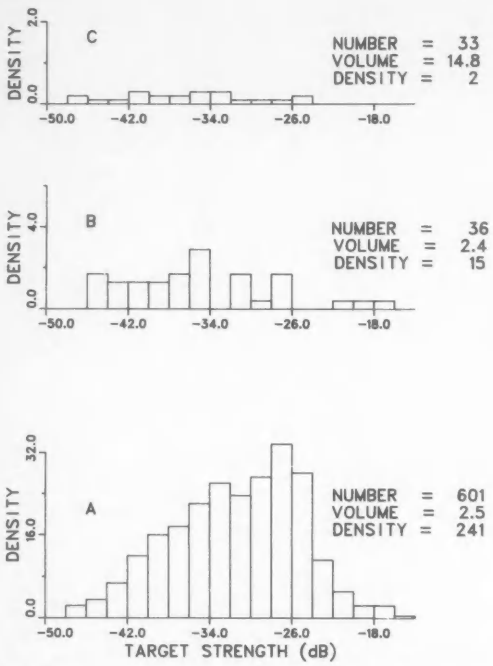

FIG. 4. Density distribution of target strengths from an acoustic transect 11 km long. Densities are numbers in a unit volume of 10^5 m^3. Frequency distributions are given for discrete water layers: A, Bottom to 3 m off bottom; B, between 3 and 6 m off bottom; C, between 6 and 30 m off bottom.

Special considerations are involved in the process of defining the difference between a fish echo and a bottom echo. In designing and choosing equipment and signal sensitivities we have taken pains to generate fish and bottom echoes which rise as quickly as possible to their peaks and decay similarly quickly. However, completely rectangular envelopes are an impossibility. It must therefore be recognized that there will be a measurable rise time up to the relatively high level of the bottom echo, particularly where the surface of the sea bottom is soft or sloping. Fish echoes may be obscured in this rise time. Difficulties caused by this phenomenon in sampling the bottom water layers helps to dictate the adoption of generally small beam angles which reduce the likelihood that fish may be lost at the edges of the cone cross section. In this analysis our interpretative program examines the sequence of signals in the rising bottom echo. We identify a fish in this sequence if a submaximal peak occurs in it.

Results

Target Strength Distributions in Relation to Size Compositions of Fish Catches

During the experimental cruises, sequences of acoustic transects with ECOLOG were interspersed with net hauls. In illustrating the relationships between results of the two sampling methods we have initially chosen examples of acoustic transects which are as close as possible to net tows in space and time.

In Fig. 4, A–C, we reproduce the target-strength frequency distribution for a transect begun at 12:21, Feb. 5, 1981. The transect was ~11 km long, and required about 86 min to complete. The bottom depth is known for each transmission and averaged about 70 m below the transducer with very little variation, hence the transect path was ~8 m wide at the bottom. In Fig. 4A the average depth was used to calculate the volume of water sonified in a layer 3 m above the bottom, corresponding to approximately the water layer sampled by the otter-trawl. We have also calculated the volumes sampled between 3 and 6 m (Fig. 4B) and between 6 and 30 m (Fig. 4C) off bottom. The acoustic information has been compiled separately for each of these layers. The resulting calculations of numbers of individual fish of each target strength are plotted in terms of fish density within each target strength size-class per unit volume of water sonified (i.e. number per 10^5 m^3). Target strengths are displayed on an arithmetic scale of decibel levels in size-classes of target strength taken over 2-dB intervals. To the extent that variations in target strength reflect fish sizes, it appears that the bulk of fish occurred in the bottom 3 m and was made up of relatively larger fish, with a mode at −27 dB. Relatively few and smaller fish were detected between 3 and 6 m off bottom and almost none were detected in the rather large volume of water sampled above 6 m from bottom.

With the relatively small beam widths used, the sampling transect is narrow and the high volume is stretched over a long distance. Because of this, we show in Fig. 5 a three-dimensional plot in which the aggregated target strength–frequency distribution data of Fig. 4A have been recompiled and displayed for successive 100-m segments of the whole transect. As one might expect, the distribution of individual targets appears to be far from random and there is a distinct clustering of different target-strength classes at different positions along the transect. In fact, as will be discussed in more detail later, if the total transect is divided into 3 approximately equal sections, the measured heterogeneity between sections is significantly greater than within sections. Such results are consistent with the expectation that variations in small-scale fish distributions are size-dependent. The clustering of target strength along the transect therefore supports the idea that it should be possible to interpret the target-strength differences as fish-size differences.

With the equipment immediately available to us, as with most fisheries research laboratories, the otter-trawl provides the most direct approach to verifying the source of the variations in target-strength distributions. In Fig. 6A we present the size-composition of the total catch of fish (mostly haddock) made in two replicate 30-min tows run parallel to the acoustic transect and as close to the middle of that transect as could be managed. In fact, the tows were made in succession first, beginning at 09:00 and ending at 11:30, ~1½ h before the acoustic transect passed through the area. The distance covered by the net was about ⅓ that of the acoustic transect. We calculate that the path width effectively swept by the trawl

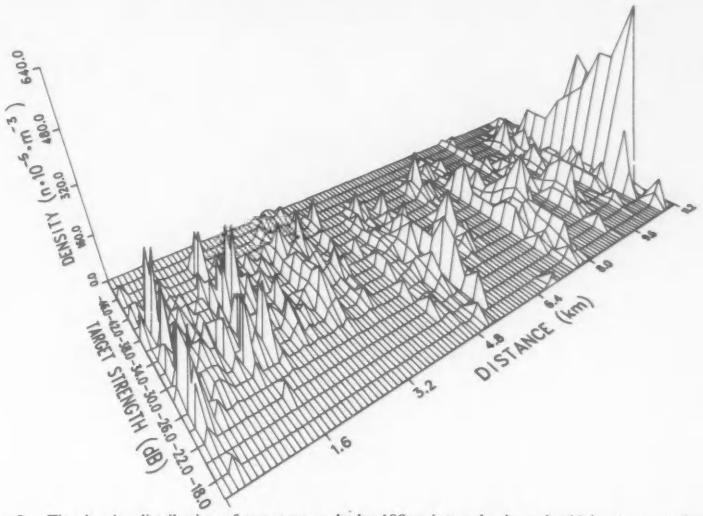

FIG. 5. The density distribution of target strengths by 100-m intervals along the 11-km transect shown in Fig. 4.

was equivalent to ~3 times the average path width of the bottom 3 m of the sound cone. We therefore sampled roughly the same water volumes in each ½-h tow and in the 11-km transect. The catch data are plotted as number per 6-cm size-class per 10^5 m^3 of water for comparison with the acoustic results. There was considerable variation in apparent fish density between the tows, the second yielding only about half the total catch of the first, although both yielded about the same size-composition. Overall densities in the acoustic transect (Fig. 4) appear to be about the average of the two tows. Judgment of the significance of the apparently higher relative proportion of the intermediate target strength fishes in the transect results depends on converting the data sets into common terms.

To effect the conversion to common terms we have chosen to use the experimental results reported initially by Nakken and Olsen (1977) and further interpreted by Foote (1979). These authors carried out a set of observations of target strengths of several species over a wide size-range at two sound frequencies, and also published plots of the original data. Their results show that for a given fish aspect, target strength is a linear function of the logarithm of fish size.

In using the experimental results as a nomogram to convert fish size to target strengths we have assumed that our fish targets would be in "average dorsal aspect." We have also assumed that experimental data derived from cod at 38 kHz could be used to interpret haddock data obtained by our 50-kHz sounder. The conversion equation for the nomogram is that given by Foote (1979) for tilt angle −4.4°. The limitations imposed by our assumptions are discussed below.

The experimental data of Nakken and Olsen (1977) demonstrate that even immobilized experimental fish may give different target strength measures on repeated observations, and Foote (1979) has published the detailed data points. These data allow us to calculate confidence interval contours (appropriate to individual prediction) around the average experimental target strength−fish size relationships. Using these contours we apportion the frequency of fish in each 2-dB size-class over the range of target strength categories indicated by probability levels established by the confidence bands. The resulting data summed within the target strength classes adopted for the acoustic transect are displayed in Fig. 6B. As might be expected, the logarithmic relationship, together with the confidence band probability distributions, has aggregated the size-classifications in a slightly different manner from the arithmetic plot and has smoothed the data without, however, losing their distinctive features. Comparison of the converted catch data with the acoustic transect shows that their basic similarity is also preserved, although with the conversion it can be seen that the modal size in the acoustic transect results was slightly higher than in the catches. The results confirm the somewhat higher proportion of intermediate sizes of fish in the transect data.

In the foregoing comparison we have carried out calculations of size-compositions on samples in which water volume was held constant. However, the shapes of the sampled volumes are quite different, as the trawl and ECOLOG sampled geographically somewhat different water masses. The geographic heterogeneity displayed in Fig. 5 suggests that this may be a major source of variation between the samples. In fact, Fig. 5 shows that in this instance a particularly high concentration of intermediate to large-sized fish was encountered at one end of the acoustic transect, well outside the area sampled by the trawl. As a test of this possible geographic effect, we have compiled the target strength composition for that part of the ECOLOG transect that most nearly corresponds with the path of the trawl tow. The result, in Fig. 6C, shows an overall lower acoustic estimate of density, more like

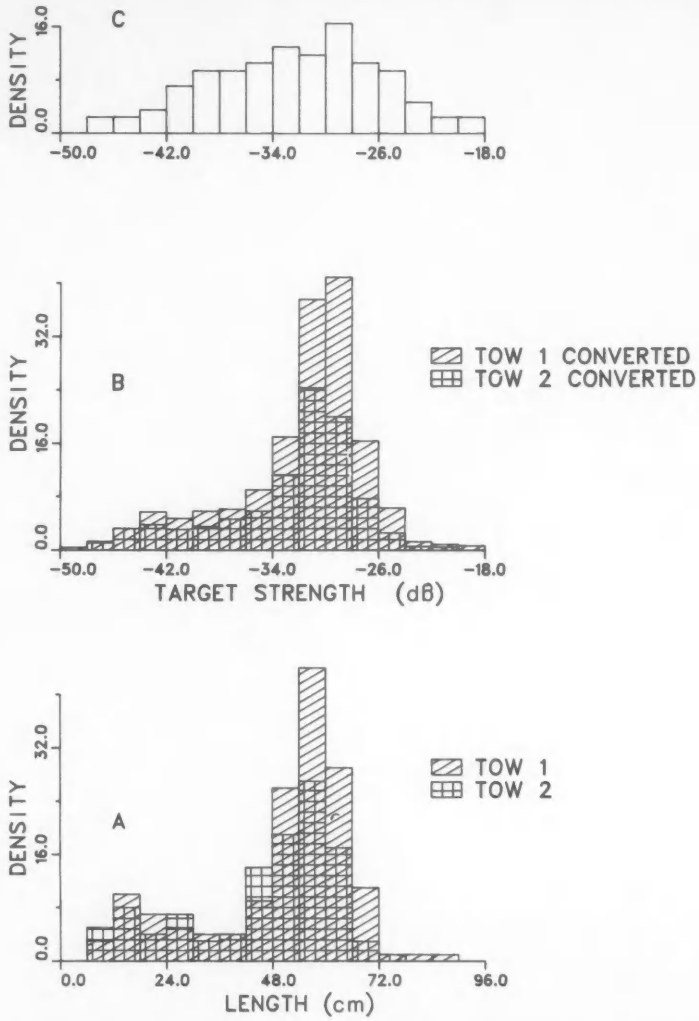

FIG. 6. A. Density distributions by length classes of two 30-min tows made in the center of the transect shown in Fig. 5. B. The tow density distributions converted to the equivalent target strength density distributions (see text). C. Target strength density distribution from the tow track area of the acoustic transect.

that encountered in the second tow, and a lowered modal size which is closer to that of the tows than of the total transect, although much reduced in relative strength.

It appears that in the acoustic data we have direct information on fish size and density within small water volumes. We may assess the validity of this conclusion and some of the limitations on the usefulness of the information by a statistical examination of the sources and magnitudes of variation within and between the two sets of sample results.

VARIATIONS AMONG THE FISH POPULATION SAMPLES

To determine the significance of the differences between the acoustic and catch target strength compositions we have carried out a three-dimensional analysis using the Information Statistic which is equivalent to the χ^2 test (Kullback 1968). For this purpose, the target strength–class frequencies of the various samples are taken as rows (R), and arranged

TABLE 3. Information statistic analysis of variances. df = degrees of freedom, P = probability level of significant heterogeneity. (* = 0.05, ** = 0.01, ns = 0.05.)

Part	1				2				3				4			
Third-dimension term	Tows vs. total transects				Tows vs. ¼ transects				East, middle, and west sections of successive replicate transects				Day and night classification of the sections of selective transects			
Line term	df	Info.	χ^2/df	P	df	Info.	χ^2/df	P	df	Info.	χ^2/df	P	df	Info.	χ^2/df	P
Total variation R×C×D	80	290.2	3.63	**	80	276.8	3.46	**	127	472.2	3.72	**	126	1149.9	9.13	*
A. Due to arrangement in size-composition (R×C)	33	31.1	0.94	ns	33	30.0	0.91	ns	33	113.7	3.45	**	55	140.3	2.55	**
B. Due to classification D×(R,C)	47	259.1	5.51	**	47	246.8	5.25	**	94	358.5	3.81	**	71	1009.6	14.22	**
C. Between classes D-Homo.	3	46.3	15.46	**	3	15.5	5.15	**	6	197.3	32.89	**	5	118.8	23.76	**
D. Within classes Cond (R/C)	44	212.8	4.84	**	44	231.3	5.26	**	88	161.2	1.83	*	66	890.8	13.50	**
E. Among samples R,C-homo.	11	183.1	16.65	**	11	188.7	17.15	**	22	18.0	0.82	ns	11	805.3	73.21	**
F. Sample homogeneity R,C,D-int.	33	29.7	0.90	ns	33	42.6	1.29	ns	66	143.2	2.17	**	55	85.5	1.56	ns

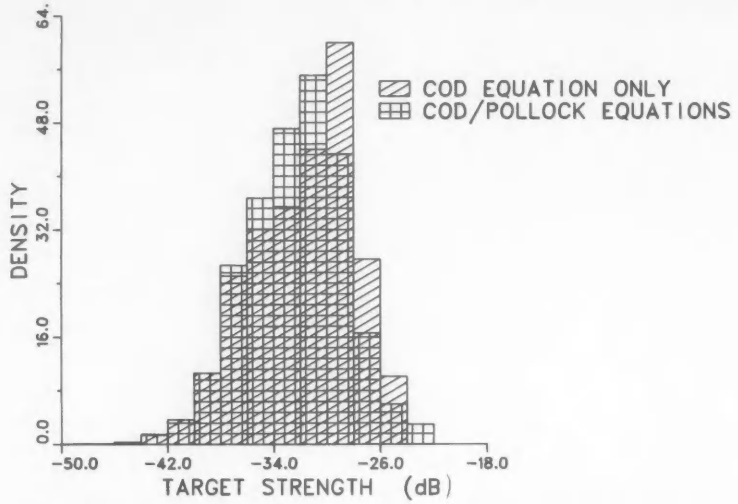

FIG. 7. Target strength density distributions for one tow using different nomograms to convert fish lengths to target strengths (see text).

in columns (C) representing "replicate" samples of a given classification. This two-dimensional array of samples is then compared with one or more other arrays in the depth (D) dimension. Appropriate marginal totals are determined and all entries in the three-dimensional tables are replaced by the "information" term ($x \ln x$). Methods of calculation are given in detail by Freeman and Dickie (1979).

The results of several such analyses are summarized in the 4 parts of Table 3. In the first line, under the heading "Info" is given the total measured variation within the data set (R×C×D). This is partitioned into its two principal components: in line A the variation accounted for by the size-composition arrangements (R×C), and in line B the interaction of the size-composition arrays with the "depth" classification (D×(R,C)). The variation in row B may itself be partitioned. We show in row C the component attributable to the main classification into different two-dimensional arrays, that is, the "between classes" variation (D-homogeneity). The second component in row D is thus a "within classes" measure, but may also be partitioned into two components. These are shown in rows E and F. Row E provides a measure of heterogeneity among the replicates, within each of the arrays, and is thus a "within-group" error term against which to judge the relative strength of the "between class" heterogeneity in row C, in much the same way as would be appropriate in a conventional analysis of variance of "unarrayed" data. The remainder term in row F is an interaction term reflecting the overall R×C heterogeneity among all samples.

The results given in the table confirm the importance of local geographical variations in fish distributions as the major source of differences among the samples. Part 1 of the table compares the target strength compositions of fish caught in four replicate tows with four corresponding 11-km acoustic transects (i.e. equal sample volumes). The four tows were made in pairs during daylight hours of the morning on two successive days, the pair of tows being followed by a pair of acoustic transects which included the tow track. Part 2 compares the same tows with the 3-km sections of the transects made in the towing area (i.e. equal and similar sample distances). Line C of these first two sections shows that in neither comparison is it likely that the differences in target strength compositions between net catches and transects arose by chance. However, comparison of the χ^2/df ratios between Parts 1 and 2 in lines C and E shows that the difference between the two sampling methods approaches the level of heterogeneity of replicates within the sampling methods only when the samples cover different distances (Part 1). When the sample distances are equal and geographically similar (as in Part 2) the difference between the sampling methods is only one third as large as within the samples. That is, when the same areas are sampled the apparent size-composition differences between transects and catches are not statistically significant. The differences between net catch and full-length acoustic transect is therefore mostly attributable to the heterogeneity of size-compositions among areas sampled.

The importance of sampling locality as a source of variation can be further appreciated by the data in Part 3. Here, the same series of replicate transects taken in the study area over 2 d has been divided into equal east, middle, and west sections of the transects. Line E in the table shows that the heterogeneity within the sections is low enough to be regarded as random variation, whereas in line C the variations between sections are very much greater and explain nearly half of the total heterogeneity in the samples. In this comparison, however, line F is also significant, signalling that in classifying these samples some other factor may have been confounded with sections of the transect to influence the size-

compositions. Hence this classification does not yield a precise measure of the relative importance of local area on heterogeneity.

This result may be followed one step further from the data collected on the experimental cruises. In Part 4 (Table 3) we have compared a set of replicate transect data made during day and night. Line C shows what appears to be an important difference between the day and night target strength distributions, although as can be seen by comparison with line E, the between day−night component is only about one-third as great as the heterogeneity measured within the arrays of day or night transects. It is to be noted that in this data set, line F shows a satisfactory level of homogeneity of the size-compositions among the day and night classes. We may therefore conclude that the day−night classification makes an important contribution to identification of the sources of sample heterogeneity, although this total heterogeneity is clearly dominated by the differences among locality.

Limitations on Interpretation

The foregoing suggests that ECOLOG is suited to a study of the parameters of variation affecting fish distributions and abundance; hence it could be used directly in surveys to determine not only abundance but also the accuracy of abundance estimates. Because of the potential practical importance of such application we review here the data so far collected, which give some indications of its limitations.

The main doubts concerning echo counting as compared with echo integrator systems are centered on the problems of coincidence counting. Our data offer at least preliminary information on this point. Of critical importance for accuracy of echo counting is interpretation of the array of interrupts such as is displayed in Fig. 3. Our definition of "single" fish generally resolves on the order of 85% of all interrupts. We have also been enabled to identify peak "voltages" which have a size-distribution not significantly different from the corresponding size-distributions of catches. This would appear to provide tentative support for two conclusions:

1) We have correctly identified and measured echo amplitudes for individual fish.

2) Fish not included in the analysis because they appear in the groups defined as "multiples" are an unbiased sample of the population.

If these conclusions continue to be supported by additional experimental data, it would appear that without further adjustment our results may give an underestimate of population density and abundance.

It might be expected a priori that the problem of "multiples," which represents a form of "coincidence counting," would be a function of overall density in the sense that it might depend on the total number of targets simultaneously appearing in the sonified cone. As one means of testing this hypothesis we have run a number of our transects at various speeds and with the transducer suspended at different depths. With the transducer high off bottom giving larger sonified cones we might expect coincidence counting to increase, hence estimates of density to decrease. However, the calculated correlation between depth and estimated density of fish on sections of the transects was in fact an insignificant positive value. At the densities of fish encountered, it appears that density is not responsible for such concidence counting as we have encountered. Because commercial fishermen using our sample area in 1981 were making considerably above average catches, it may further appear that fish densities likely to be encountered on demersal fish surveys will not be a problem limiting the use of ECOLOG.

We have also calculated the correlation between "multiples" and estimated densities in transect sections. There is again a positive but insignificant correlation. We conclude that our problem of "multiple" echoes is a function of small-scale aggregations of fish, and is therefore related to behavior, rather than population density per se. If this conclusion is confirmed it would seem that the most appropriate direction for refinement of our present estimates lies in manipulation of our definitions of "single" fish, or simple corrections based on the fraction of interrupts included as multiples.

There remain a number of problems associated with the choice of appropriate nomograms and confidence intervals for the conversion of fish sizes to corresponding target strengths. Such problems are, of course, common to echo counters and integrators. In our analysis we chose to use the Nakken and Olsen (1977) data as edited and adjusted to averaged dorsal aspect by Foote (1979). The results provided satisfactory interpretations of the target strength−size frequencies. Such data can be collected in the field only by echo counters and loggers of the type we use, and the results assure us that the experimental results have application to the field surveys. Alternative estimates of fish size−target strength relations are available, e.g. the Nakken and Olsen data (1977) adjusted for "field conditions," or Buerkle and Sreedharan's (1981) estimate. Both give satisfactory overall shapes for the size distributions, although small differences appear in the apparent modal size-classes. This subject clearly requires further investigation with ECOLOG, but it would appear that the existing information provides a satisfactory starting place.

The problem of the effects of multiple species on acoustic signals has been considered by a number of authors. Foote (1979) points out that his average curves for various demersal species and for different transmission frequencies differed significantly from one another. In Fig. 7 we show two target strength−frequency histograms for a catch of mixed pollock and haddock made in October 1980. One histogram is derived by applying the Foote cod equation to the entire catch. The other applies the cod equation to haddock and the pollock equation to the pollock. There is a difference between the two distributions, but this appears minor compared with the distribution differences we have encountered for a single species in different parts of the transects. The two nomograms we used for Fig. 7 represent the extremes in demersal species analyzed by Foote, and we have applied it to the extreme in "mixed" species on our experimental cruises. It seems fair to conclude from this that subsampling of acoustic transects for species composition may result in refinement of biomass estimates, but that strong arguments could be made in survey design in favor of sacrificing such refinement for the sake of increases in the area sampled. Relative costs and benefits should be calculable for particular situations and objectives.

Finally, it is appropriate to take note of evidence for the effects of fish behavioral differences on acoustic estimates.

Our data (Part 4, Table 3) showed that there was a significant difference in the apparent size-compositions encountered in transects during day and night. There were also day–night differences in overall density and in the distribution of fish throughout the water column. All of these effects are already well known from previous research and fishing experience. Our principal new contribution to this general knowledge derives from the fact shown in Table 3 that division of our transects into day and night samples was necessary to create homogeneous subsamples for study. The coincidence of the apparent change in size-composition with changes in water column distribution makes it appear that we may be dealing here with effects of fish aspect and movement, already studied in some detail by Nakken and Olsen and Buerkle and Sreedharan, rather than actual change in sizes in the population. Our data suggest that further efforts to understand these effects are essential. Meanwhile it appears that acoustic surveys should treat day and night information as different sets of samples.

Conclusions

The most important item of information which has been missing from acoustic survey interpretation is the target strength of fish under field conditions. The foregoing analysis of ECOLOG data indicates that this deficiency can be overcome for demersal fishes and that, in fact, results already obtained in laboratory experiments are very close to what is required. With this assurance, it is a small extension to use acoustic systems based on the echo-counting principle to study fish behavior and microdistribution, and to develop this information for estimates of abundance and of catch rates.

Our limited experience suggests that this further development is itself close to realization. The data suggest that problems with coincidence counting are probably not directly correlated with density at the levels commonly encountered for demersal fishes. It also appears that such coincidence counting as can be identified does not appear to bias the size-composition samples. By contrast, our information supports previous speculation that diurnal rhythms may involve behavioral patterns that affect apparent size-compositions. Until these are better understood it appears that acoustic results may require day–night stratification and probably require different conversion factors.

The most outstanding result of these preliminary experiments is the evidence for very high local spatial heterogeneity in population size-distributions. Heterogeneities of a comparable order were found among commercial samples of demersal fishes in early studies by Dickie and Paloheimo (1965), who suggested that they create problems in sampling for population parameters. It is clear for the situations studied here that research vessel surveys are liable to strong local effects and that the 30-min tow duration often favored for such surveys may be rather poorly suited to give representative population samples. This indication is strong enough to require further priority study.

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Early Growth and Quality of Chum Salmon (*Oncorhynchus keta*) Produced in Keeper Channels and Gravel Incubators

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BAMS, R. A. 1983. Early growth and quality of chum salmon (*Oncorhynchus keta*) produced in keeper channels and gravel incubators. Can. J. Fish. Aquat. Sci. 40: 499 – 505.

Chum larvae were incubated in two types of incubation system — a pilot Japanese-style hatchery (JSH) and a set of deep-gravel incubators (box) — at two levels of flow and two, or three, levels of egg density. Following voluntary emergence, fish were reared in tanks on an OMP diet and their growth rates compared. Initially, fry from both systems were of the same average size, but the JSH fish emerged 6 d earlier than the box fish and at a stage of development 6 d less advanced. At the end of 8 wk, all JSH groups were significantly longer than the box groups; the most extreme groups averaged 63.4 and 59.2 mm, respectively. Not only had the JSH fish kept their 6-d lead in additional growth, but they also grew significantly faster (calculated average rates were 3.553 and 3.217 mm/wk in the above groups). A previous assessment of fry quality had rated the JSH fry inferior to the box fry on the basis of four criteria (efficiency of yolk conversion, size and stage of development at emergence, and time of emergence). In this test, however, JSH fry rated superior in terms of final size and rate of growth achieved during 8 wk following emergence. Difficulties with simplistic quality criteria and how such criteria relate to fitness are discussed.

BAMS, R. A. 1983. Early growth and quality of chum salmon (*Oncorhynchus keta*) produced in keeper channels and gravel incubators. Can. J. Fish. Aquat. Sci. 40: 499 – 505.

Des larves de saumons keta ont été incubées dans deux systèmes d'incubation — une écloserie-pilote de style japonais (JSH) et une série d'incubateurs (boîtes) avec couche profonde de gravier — à deux niveaux de débit et deux ou trois niveaux de densité d'oeufs. Après émergence volontaire, les larves ont été élevées dans des bassins à un régime alimentaire OMP, et les taux de croissance comparés. Les alevins incubés dans les deux systèmes étaient de même taille moyenne au début, mais les poissons de JSH émergèrent 6 jours plus tôt que ceux incubés dans les boîtes, et à un stade de développement en retard de 6 jours. Après 8 sem, tous les groupes de JSH étaient nettement plus longs que les groupes des boîtes; les longueurs extrêmes étaient en moyenne de 63,4 et 59,2 mm respectivement. En plus de maintenir leur avance de 6 jours de croissance, les poissons de JSH eurent également une croissance significativement plus rapide (les taux moyens calculés ont été de 3,553 et 3,217 mm/sem dans les deux groupes). Lors d'une évaluation antérieure de la qualité des alevins, on avait jugé ceux de JSH de qualité inférieure à celle des alevins éclos dans des boîtes, sur la base de quatre critères (rendement de conversion du vitellus, taille et stade de développement à l'émergence et moment de l'émergence). Dans la présente expérience, cependant, les alevins de JSH ont été jugés supérieurs, quant à leur taille finale et taux de croissance atteint dans les 8 sem qui suivirent l'émergence. Nous examinons les difficultés que causent des critères simplistes de qualité et la façon dont ces critères reflètent la condition physique.

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THERE is continuing interest in what is commonly and loosely referred to as fry and smolt "quality" or "fitness," in particular of hatchery-produced salmonids (e.g. Vibert 1958; Bams 1967; Burrows 1969; Koski 1975; Poon 1977). Rigorous ecological argument must recognize general fitness (survival capacity) expressed over the long term, certainly as far as the reproductive stage, if not beyond. In the case of a Pacific salmon fry, for example, ultimate fitness may be expressed simply and logically as the number of offspring it will eventually produce and, thus, should include the survival rate of its progeny while in the gravel insofar as this is dependent on parental choice of optimal nest-site parameters. Such an ultimate-type argument is obviously a variant of R. A. Fisher's (1958) original definition: "... fitness [is measured] by the objective fact of representation in future generations" but it is more of theoretical importance than of practical help to a fish culturist.

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Clearly, more proximal measures of fitness would be useful from a practical point of view, even though such "working" measures would be restricted in time, place, or biological function. Thus robbed of its broad, evolutionary, ecological sense, the term fitness becomes inappropriate, even though it is common parlance in the fish-cultural field. It seems prudent to use the less precise word quality instead, and use fitness only in more appropriate contexts, e.g. fitness components. The restricted criteria approach is obvious in Koski (1975), who defines a "useful" fry quality measure according to life stage: "the fitness of salmon fry at emergence refers to their capacity to survive the transition from the freshwater environment to the marine environment and to survive to the juvenile stage where perhaps a new set of fitness components are (sic) required." One can conceive of many such sets of fitness components dealing with a variety of properties of the animal, both instantaneous and distributed in time and space. Poon (1977) lists various components commonly used on salmonid fry and reported in the literature: morphometrics, survival, stage of development at migration, timing of migration, swimming ability, predator avoidance, resistance to stress, postemergent growth, response to light, state of nutrition, and resistance to starvation.

During the late sixties, emphasis on the quality of hatchery-produced but unfed pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon fry led to the development of several variants of the "deep-substrate incubator" (Bams 1970; Bailey and Taylor 1974; Wilson 1974). This class of incubator produces fry superior in many fitness components to fry produced in traditional hatchery baskets and trays, or in shallow-matrix systems such as the Netarts box (McNeil 1969) and the Japanese-style keeper-channel incubators (Moberley and Lium 1977; Helle 1979). In an experiment comparing his deep-substrate technique with variants of the traditional Japanese-style channel technique, Bams (1982) established the superiority of box fry, in terms of yolk conversion efficiency, size and stage of development at emergence, and timing of emergence. The experiment presented here is a continuation of this quality evaluation.

The "standard" Japanese-style chum hatchery accelerates the development of the brood during incubation by the use of groundwater. A period of 6–8 wk is thereby gained in the spring in which the fry can be fed heavily. Such fry reach a size of 1–2 g at the time of migration normal for the naturally propagated fry. That such "enhanced" fry can compete successfully with natural fry comes as no surprise. What has not been evaluated is the possibly advantageous effect of a different incubation technique — up to the time feeding starts — on growth following emergence. This experiment was therefore designed to compare growth, following emergence, of several groups of fry produced in Japanese-style keeper channels and in deep-gravel incubators. The end point of the experiment was preset, i.e. analogous to a fixed release date as set in hatchery practice.

Methods

A pilot Japanese-style hatchery (JSH), located at the Rosewall Creek fish-cultural facility (Dep. Fisheries and Oceans), 80 km north of Nanaimo on the east coast of Vancouver Island B.C., was modified to contain four rows of six experimental units each. The units measured 1.4 m long by 0.8 m wide, and were separated by stainless steel screens; water depth was set at 15 cm. Fertilized and water-hardened eggs were obtained on December 3, 1979 from the Big Qualicum chum stock and transported to Rosewall Creek. At

TABLE 1. Average chum fork lengths (mm) at weekly intervals, by incubation group and tank color. (n = 50, with one exception where n = 49.)

			Week[a]							
Group[b]	Color[c]	No.[d]	1	2	3	4	5	6	7	8
I	G	12	39.23	41.86	44.85	48.63	51.70	56.71	59.46	62.97
	A	20	38.66	41.28	45.11	48.01	53.55	56.83	59.35	62.54
II	G	11	38.79	42.16	44.99	48.84	52.99	56.54	59.63	64.38
	A	16	38.99	42.10	45.74	49.48	53.53	56.62	59.61	62.11
III	G	15	38.66	42.31	45.01	49.45	53.22	56.96	59.75	63.65
	A	9	39.17	41.53	45.50	48.87	53.43	56.11	59.72	63.14
IV	G	14	38.88	41.51	44.28	48.23	51.65	56.42	58.66	62.67
	A	18	38.89	41.53	45.28	49.23	51.90	56.69	59.84	62.28
V	G	13	37.27	39.29	41.59	44.90	49.41	53.19	55.50	59.22
	A	19	37.16	40.00	42.06	45.35	48.93	52.91	55.21	59.20
VI	G	10	36.59	39.32	41.81	46.25	49.59	52.85	56.91	58.73
	A	17	36.92	39.55	42.55	45.44	49.59	53.26	55.90	59.63
Pooled	G	—	38.24	41.08	43.76	47.72	51.43	55.45	58.32	61.94
	A	—	38.30	41.00	44.37	47.73	51.82	55.40	58.27	61.48

[a]Week 1 ended April 23, 1980.

[b]Group I = JSH D_1F_1; II = JSH D_2F_1; III = JSH D_3F_2; IV = JSH D_3F_1; V = Box D_1F_1; VI = Box D_3F_2.

[c]Color = rearing tank color, where G = dark green, A = light aquamarine.

[d]No. = tank number.

TABLE 2. Analysis of covariance of mean lengths on six groups, two rearing tanks, eight successive weekly intervals.

Source	SS	df	MS	F	P	
Groups, I/VI	210.890	5	42.118	99.08	0.000	***
Tanks, G/A	0.086	1	0.086	0.20	0.655	ns
Interaction	0.865	5	0.173	0.41	0.843	ns
Regression	5938.603	1	5938.603	13950.80	0.000	***
Error	35.332	83	0.426			

the eyed-egg stage all units were charged at one of three densities, $D_{1.2.3}$ = 6000, 12000, 24000 eggs/m^2; and at one of two flows, $F_{1.2}$ = 20 or 40 L/min (approximate linear velocity 33 or 66 cm/min). The water supply was pumped and aerated groundwater. Temperatures in all units ranged from 8.1°C at hatching to 7.3°C at emergence. Dissolved oxygen of the incoming water was near saturation, that of the outflow reached minima of 8.83 mg/L in the low flow and 9.32 mg/L in the high flow channels. Un-ionized ammonia ranged from 0 in the inlet water to 0.146 μg/L (highest recorded) in the outflow.

Another group of eggs, with identical history to planting, was incubated to the migrant fry stage in four small (0.3 × 0.6 × 1.2 m deep) deep-gravel incubators. These incubators were identical with the usual 4 × 8 ft (1.2 × 2.4 m) models (Bams and Crabtree 1976) in all respects except size and were operated at D_1F_1 and D_2F_2, where $D_{1.2}$ = 16000 and 32000 eggs/unit, and $F_{1.2}$ = 8 and 16 L·min^{-1}·unit^{-1}. These treatments represent "standard" and two times standard density and flow levels. Details of design, operation, and results of this experiment are available in Bams (1982).

Following incubation and self-release, four groups of fish, each replicated once, were obtained on April 11 and 12, 1980, from two each (combined) of the following channel (JSH) treatments: D_1F_1, D_2F_1, D_3F_1, and D_3F_2 at the midpoint of these runs. All these channel treatments had a single layer of gravel. Two additional groups, also replicated once, were obtained from the replicated deep-gravel incubators (Box): D_1F_1 and D_2F_2. Because the treatments had caused significantly later emergence from the box units, the box-fry groups were not obtained until April 17 and 18, i.e. on average 6 d later than the channel fry, at about the 20% point of the runs.

Fry sizes had been established on preserved samples of 50 fish each from all incubation units as part of the evaluation test. For the channel fry 16 samples were available, from the 8 units used on the two collection dates; these showed a range of fork length means of 35.78–36.72 mm, with an arithmetic mean of 36.27 mm. For the box fry eight samples were available from all four units but with one sampling day preceding the collection day by 1 d. These lengths ranged from 35.75 to 36.70 and had a mean of 36.24 mm. Although the overall population mean lengths differed significantly (Bams 1982), the means and ranges of the two groups of fish collected for this experiment were virtually identical. Although there was no significant difference in the starting sizes, the JSH fry were at a significantly earlier stage of development than the box fry. On the same samples it was established that the developmental index, K_D (Bams 1970), of the JSH fry ranged from 2.022 to 2.068 with a mean of 2.043, whereas that of the box fry ranged from 2.012 to 2.033 with a mean of 2.021. This reflected a difference of about 6 d of development at the prevailing temperatures.

TABLE 3. Regression analysis of mean lengths of all six groups, replicated, sampled eight times, at weekly intervals. Groups are ranked by decreasing slope value.[a]

Source	Group	n	a	b	SE(b)	r
JSH-D_3F_2	III	16	35.035	3.5538	0.048	0.999
-D_2F_1	II	16	35.191	3.5200	0.061	0.998
-D_1F_1	I	16	34.840	3.5181	0.070	0.997
-D_3F_1	IV	16	34.853	3.4750	0.066	0.997
Box-D_2F_2	VI	16	32.902	3.3119	0.057	0.998
-D_1F_1	V	16	33.098	3.2171	0.075	0.996
Pooled	I/VI	96	34.320	3.4326	0.072	0.980

[a]Confidence limits (α = 0.95) on b are for Group III: 3.4390–3.6685; IV: 3.3067–3.6492; V: 2.9824–3.4518.

Upon procurement, each group of exactly 2000 fry was transferred to a Fiberglass rearing tank (Alderdice et al. 1966) 51 × 112 × 42 cm deep and holding ~190 L of water. Two kinds of tanks had to be used, differing only in inside (gell coat) color. One was a fairly dark green (G) and the other a much lighter aquamarine blue (A). One replicate was assigned to each color to test for any effect of color on growth. Groups were assigned at random to the six tanks in each color group. All tanks were set up together inside a building with mixed natural and artificial lighting. Water supply was the same as for the incubation experiment, and temperatures during the 8-wk period varied from 7.3 to 8.0°C.

Fish were sampled weekly before the day's feeding began, starting on April 23, by crowding them together in the tank and removing a scoop of fish. Exactly 55 of these were killed in 10% formalin, and group wet weights taken after 1 h. Individual fork lengths were obtained in the laboratory, about 3 mo later. The wet weight measure was used to calculate growth rates comparable with those reported in the literature, and, during the experiment, to establish the food ration for each following week, set at 5.1% of body weight originally and gradually declining to 3.4% during week 8. Fish were hand-fed a commercial diet, Oregon Moist Pellets, 5 times daily, starting with "mash" size for 8 d only, followed by a 50/50 mix of mash and 1/32 size for 10 d in the JSH fish but due to an oversight for only 4 d in the box fish. All groups were fed the same subsequently. Mean pellet sizes were gradually increased to 1/16 size in the final week. The fish were usually fed 20% over chart rate. No selective mortality occurred over the 8 wk; final $\bar{n}$ = 1536 ± 2.5% maximum.

The data were analyzed in part using statistical routines contained in the VAX-adapted Health Sciences Computing Facility, University of California, Los Angeles, CA, programs BMDP 1R, 1V, and 2V. These and additional routines used are in Sokal and Rohlf (1981). Nonparametric tests used are from Siegel (1956).

Results

Average fork lengths (mm) for eight weekly samples of all 12 groups ranged from 36.59 to 39.23 in week 1, and from 58.73 to 64.38 in week 8 (Table 1). In order of decreasing

TABLE 4. Analysis of covariance on all six groups, replicated, sampled eight times at weekly intervals.

Source	df	SS	MS	F	P
Group means	5	210.890	42.178	103.464	0.0000
Regression	1	5938.603	5938.603	14567.539	0.0000
Error	89	36.282	0.408		
Equal slopes	5	7.765	1.553	4.575	0.0010
Error	84	28.516	0.340		

average size in week 8, the groups rank order was III, II, I, IV, VI, and V (also see Table 5). Standard errors varied with the mean, from 5.02 in week 1 to 9.32 in week 8. The length data were not transformed, however, because regressions (on time) were calculated on the means and were virtually linear (cf. Table 3, coefficients of correlation by group $r \geq 0.996$).

To determine tank color effect (G/A) an ANOVA was carried out (Table 2). Clearly, after removal of the regression effect, differences among groups (I–VI) were highly significant ($P = 0.000$), but differences due to color (tanks, G/A) and to groups × tanks interaction were both negligible ($P > 0.06$). Subsequently, the two color treatments were treated as simple replications.

Regression analysis by group (Table 3), showed narrow ranges in intercepts (a) and slopes (b) of the six groups. The 95% confidence ranges of all six slopes overlap. However, ranking the groups in decreasing order of slope separates them by flow ($F_2 > F_1$) and by incubator type (JSH > Box), but only marginally, if at all, by density.

To establish statistical significance of differences among group means and/or slopes of all six groups, an ANCOVA (Table 4) was run. This test established, in addition to the pronounced regression effect, a significant group means effect ($P = 0.0000$) and also a significant but much smaller slope effect ($P < 0.0010$) (as indicated by the MS and F-values).

A Student-t ANCOVA analysis on (adjusted) group means established t-values for the 15 paired comparisons and their level of probability (df = 89) (Table 5). All JSH combinations (I–IV) separated clearly from the Box sources (V, VI) (all $P = 0.000$), whereas among the JSH sources only the highest density, low flow group, D_3F_1 (IV), was statistically different ($0.05 > P > 0.01$) from two other treatments, D_3F_2 (III) and D_2F_1 (II).

Daily growth rates (in millimetres per day), based on calculated length means and slopes over the 8 wk, and ranked by group as in Tables 3 and 5, were as follows.

Group III	0.444 mm/d	0.871 % (Length)/d
II	0.440	0.862
I	0.440	0.868
IV	0.434	0.860
VI	0.414	0.866
V	0.402	0.845

Absolute growth rates decreased systematically but maximally by only 6.3% (group V) from their mean; relative growth rates differed even less, by only 2% (group V).

Growth in wet weight is shown on Table 6 for the three selected groups spanning the available range. Data are normalized to the usual ln wt form. Great similarity with the length data is obvious in location of means, origins, and slopes (Fig. 1). The slopes do not differ significantly (Table 6), but the trends are the same and are also reflected in the daily growth rates, which were highest in JSH fish from the fast flow and lowest in all box fish.

TABLE 5. Group matrix arranged in decreasing order of mean length ($\bar{L}$) and slope, showing (adjusted) mean lengths, slope, covariance Student-t (above diagonal), and probability (below diagonal) values where df = 89. Underscores indicate groups mutually separated at $P = 0.05$, but not within.

Groups	III	II	I	IV	VI	V
$\bar{L}$	51.03	51.03	50.67	50.49	47.81	47.57
Slope	3.554	3.520	3.518	3.475	3.312	3.217
Group III	1.0	−0.019	1.575	2.378	14.270	15.294
II	0.985	1.0	1.595	2.398	14.289	15.314
I	0.119	0.114	1.0	0.803	12.695	13.719
IV	0.020	0.019	0.424	1.0	11.892	12.916
VI	0.000	0.000	0.000	0.000	1.0	1.024
V	0.000	0.000	0.000	0.000	0.308	1.0

Growth in length and weight can be calculated for rearing periods of equal length, compensating for the 6-d difference in initiation of rearing between the two main treatment groups. For an exact 8-wk rearing period on the above three groups we obtain the following means and 0.95 confidence limits.

Group	III	IV	V
Untransformed length (mm)	61.18(±0.42)	60.42(±0.63)	59.52(±1.02)
Back-transformed weight (mg)	2346(2220–2480)	2216(2092–2348)	2212(2039–2401)

Although the differences are attenuated, the trends observed before adjustment are still evident: the box fish (group V) are still smallest, in length significantly so.

Discussion

The experiment has demonstrated that the relatively inefficient (in terms of alevin growth) Japanese-style incubation technique did not extract a penalty in subsequent growth, at least during the first 8 wk of rearing, when compared with the more efficient deep-gravel incubation technique. On the contrary, rate of growth in length, as well as in weight was somewhat greater for all channel fish than for the box fish. This result was unexpected as comparisons made at the emerging fry stage had favored the box fish consistently and led to the expectation of superior growth among box fish following emergence as well.

The greater size achieved by the channel fry at termination of the experiment was primarily attributable to their earlier emergence and, hence, the longer feeding period available to them. Thus, rather than being a liability, the premature emergence of the channel fry turned out to be an advantage by lengthening the available period for growth resulting in a larger fish at the fixed time of release.

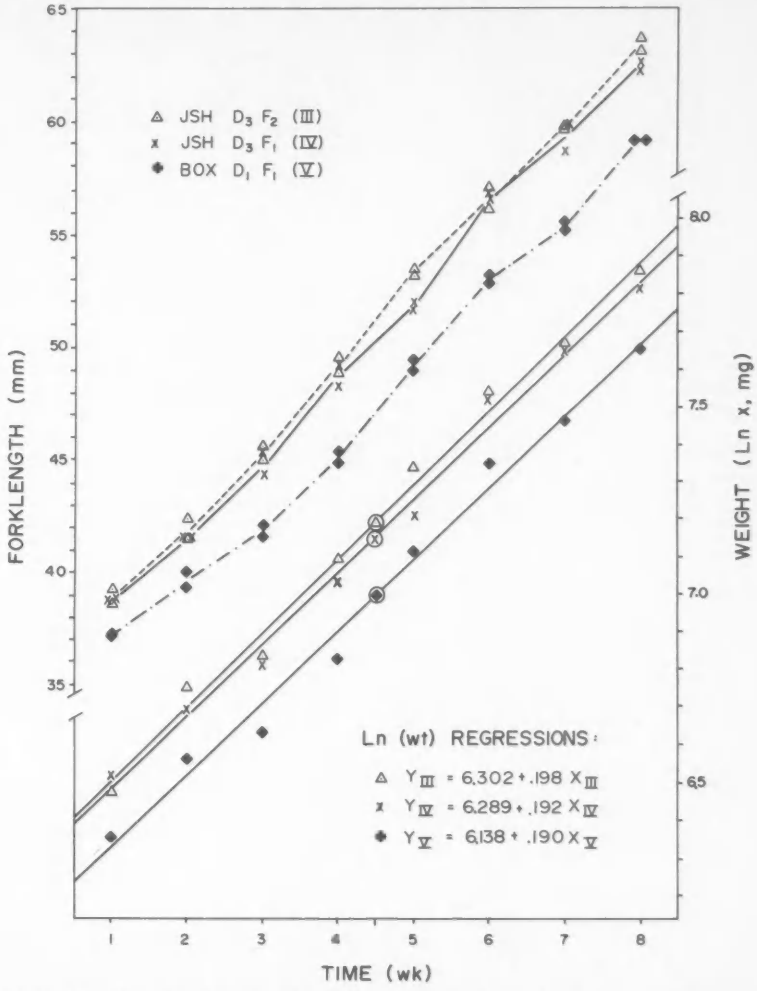

FIG. 1. Sample mean lengths (each replicate) and weights (mean of two replicates) for three experimental groups of chum fry at 8 successive weeks. Regression equations (weights on time) are included. For codes see Table 1.

Normally, *Oncorhynchus* fry initiate feeding following voluntary emergence from the gravel when maximum larval wet weight (MLWW) is reached (Harvey 1966; Bams 1970; Heming 1982). Experimental initiation of feeding at times other than MLWW have produced variable results in different attempts. Harvey (1966) noted a 10% increase in weight in sockeye fry at MLWW when feeding with freshwater plankton and brine shrimp larvae was initiated at 330, 220, and 110 t.u. (temperature units above 0 C, in C°) before normal time of swim-up. This initial gain could no longer be detected, however, after feeding was continued for several weeks. Further, fish reared similarly but on an artificial diet, containing ground liver and salmon meal, showed no increase in size at all. Hurley and Brannon (1969) found no increased growth among sockeye fry fed an artificial diet starting at 222, 111, and 55 t.u. prior to swim-up. Reinterpreting their data, however, I calculate a significant ($\chi^2 = 12.41$, df = 3, $P < 0.01$, by Friedman two-way ANOVA) average increase of some 13% in three groups of seven samples each, to 888 t.u. or about 8 wk after swim-up, when compared with the group started at MLWW. This is in good agreement with Harvey's results. Growth rates of groups starting later were believed to

TABLE 6. Average chum weights (ln wt, in mg) at weekly intervals, weekly differences (△, in %) between groups III and V, and regressions,[b] for three experimental groups.

Week	1	2	3	4	5	6	7	8
Group[a] III	6.471	6.748	6.837	7.094	7.338	7.539	7.666	7.859
IV	6.516	6.693	6.809	7.032	7.206	7.518	7.647	7.814
V	6.358	6.562	6.637	6.824	7.112	7.350	7.460	7.655
Δ(III−V)	12.0	20.4	22.1	31.0	25.4	21.8	22.9	22.6
III	$\bar{Y}$=7.194(±0.035);		a=6.302;		b=0.1983(±0.0151);		r=0.9962;	G=2.83
IV	7.154	0.036	6.289		0.1923	0.0158	0.9957	2.75
V	6.995	0.043	6.138		0.1904	0.0187	0.9938	2.72

[a]Codes are as given on Table 1.
[b]$\bar{Y}$ = mean ln wt; limits of $\bar{Y}$ at α = 0.95; a = Y-intercept; b = slope; limits of b at α = 0.95; r = correlation coefficient; G = daily growth rate, %.

have been somewhat higher than those of earlier groups, thus attenuating the acquired advantage of the earlier groups.

Heming (1979) established for chinook salmon (*O. tshawytscha*) that at any of four temperatures there was no growth advantage in feeding alevins more than 40 t.u. prior to MLWW. On the contrary, because the fish were exposed to light when feeding was started, their activity levels would increase, causing their growth to consistently and significantly ($P < 0.02$, Binomial test) lag behind that of the controls, which were kept continually in the dark (my interpretation of the data). From 40 t.u. prior to MLWW on, however, feeding produced a considerable (up to about 20%), consistent, and significant advantage compared with fish initially fed at MLWW. The normal leveling off to zero growth (in wet weight), which produces the MLWW phenomenon, does not occur in the fish fed earlier; they simply maintain their larval growth rate, evidently by augmenting, to a constant maximum, their now limiting yolk supply with nourishment taken from the exogenous food source.

Our box fry were at MLWW at emergence, as is typical of well-run deep-substrate incubators, whereas the channel fry emerged more prematurely, as is typical of shallow or no-substrate incubators, in this case by about 44 t.u. Because this interval exceeds Heming's 40 t.u., application of his findings to our fry would predict that the maximum growth advantage (about 20%) would have occurred. This is in excellent agreement with the maximum average difference of 22%, established for groups III and V, Table 6.

Evidently, emergence and initiation of feeding at MLWW, as observed in nature and in deep-gravel incubators, does not maximize growth. The adaptive significance of the "late" natural emergence probably lies in enhanced immediate survival, because premature fish have reduced size, reduced swimming performance, and greater vulnerability to predation (Bams 1967; Blaxter 1969; Thomas et al. 1969).

Heming (1979) showed identical and constant growth rates (log wt) of chinook fry following the different treatments during the 8 wk covered by our experiment. He obtained rates of about 2.75 ± 0.16% per day for comparable treatments. These rates agree well with ours, which ranged from 2.72% in the box fish to 2.83% in the fastest JSH fish (Table 6). This growth is below that achieved by Shelbourn (1980), however, on chum fry of similar age, fed to excess in identical tanks and with the same diet, but at $\frac{1}{10}$ the density. Interpolation of his data yields a rate of 3.6% per day at 8°C, indicating that there was scope for additional growth in our experiment. Shelbourn expects (1980) that even greater rates can be achieved with a species-specific diet, which could be of substantial advantage in a time/temperature limited JSH operation.

Finally, the results of this experiment demonstrate a major difficulty with the use of fitness components to evaluate quality. The evidence they produce is not necessarily coherent and may well be uneven or contradictory. In our case, on the basis of four commonly accepted criteria (efficiency of yolk conversion, size and stage of development at emergence, and time of emergence), it was concluded that the box fry were superior in quality to the JSH fry at time of emergence. Yet, following rearing for 8 wk, it was demonstrated that the box fry grew at a reduced rate and achieved a smaller size than the JSH fry, not only at the predetermined fixed time of release (Table 1), but also after equal growth periods of about the same duration (text table p. 502). Therefore, evaluated by these no less acceptable criteria the box fry should be judged inferior in quality. What emerges from this is the importance of two things: (1) any fitness component must be defined very precisely, including a time or location dimension where necessary; and (2) the biological significance of any component must be viewed in relation to others and to the particular set of circumstances.

In the present experiment, judging the emerging box fry superior by the four quality criteria cited before (yolk-conversion efficiency, stage of development and size at emergence, and time of emergence) would almost certainly have been correct providing the fish of both groups had been (1) released into nature, and (2) at the normal migration time. Without these two additional conditions, however, the validity of the judgment was questionable. As shown, to emerge 6 d prematurely proved to be advantageous in the hatchery situation, because together with the availability of food this (1) increased time available for feeding and, hence, ultimate fry size, and (2) in the absence of predation and high-velocity currents it also enabled the fry to bypass the maximum-larval-wet-weight stage and thus gain additional growth. Clearly, the balance among different fitness components is complex and the search for a simple set of fry quality criteria may well prove elusive. The best we can do at present is to use such essentially simplistic criteria with care and avoid extrapolation and generalization.

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A Test of Lead-210 Dating for the Measurement of Whole Lake Soft Sediment Accumulation

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EVANS, R. D., AND F. H. RIGLER. 1983. A test of lead-210 dating for the measurement of whole lake soft sediment accumulation. Can. J. Fish. Aquat. Sci. 40: 506 – 515.

We have tested the hypothesis that variation in accumulation of soft sediments over a lake bottom is related to the lake morphometry, allowing an accurate measurement of whole lake sediment accumulation. In each of two Laurentian Shield lakes in southern Ontario, sediment accumulation was measured at ~20 locations. In both there was a statistically significant linear relationship between soft sediment accumulation and the water depth at the sample locations. The relationship explained 72 and 57% of sediment accumulation variation in Costello and Red Chalk lakes, respectively. Using these relationships, it was possible to calculate the whole lake sediment accumulation rate for each lake. The results indicate that, in general, there is a linear variation in sediment accumulation as a function of depth in small Shield lakes. This study points out the need for a closer examination of sediment movement and accumulation in the shallow regions of lakes.

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La présente étude a été menée en vue de vérifier l'hypothèse que la variation dans l'accumulation de sédiments mous au fond d'un lac est liée à la morphométrie de ce dernier, ce qui permet de calculer de façon précise l'accumulation dans tout le lac. Nous avons mesuré l'accumulation des sédiments à environ 20 sites dans chacun de deux lacs du Bouclier laurentien. On a trouvé dans les deux une relation linéaire significative à l'analyse statistique entre l'accumulation des sédiments mous et la profondeur de l'eau aux sites d'échantillonnage. La relation explique 72 et 57 % de la variation dans les lacs Costello et Red Chalk, respectivement. Grâce à ces relations, on a pu calculer, pour chaque lac, le taux d'accumulation des sédiments du lac entier. Ces résultats indiquent qu'il y a, en général, variation linéaire de l'accumulation des sédiments en fonction de la profondeur dans les petits lacs du Bouclier. Notre étude fait ressortir le besoin d'examiner de plus près le mouvement et l'accumulation des sédiments dans les régions peu profondes des lacs.

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THE mechanism of soft sediment deposition in lakes has drawn much attention recently (Hakanson 1977; Sly 1978). Largely this is because soft sediments have a high affinity for most contaminating substances (e.g. Kemp et al. 1978; Evans and Rigler 1980a).

Hakanson (1981a, b) has investigated the mechanics of movement of fine-grained sediments in shallow regions of lakes. He has produced a model to differentiate between areas of erosion, transportation, and accumulation. From his work, it is possible to calculate the lake water depth at which the soft sediments begin to accumulate. However, the work does not address the question of how accumulation rates vary over the accumulating areas. Davis and Ford (1982) examined the change in sediment accumulation at five stations in Mirror Lake, New Hampshire. They concluded that five samples were insufficient to reflect accurately spatial variation and to quantify whole lake sediment accumulation. Evans and Rigler (1980b) investigated soft sediment accumulation in a Precambrian lake in southern Ontario, by using ^{210}Pb dating. They found that sediment accumulation varied linearly with depth of lake water over the accumulating areas. Using this relationship, they were able to calculate the average sediment accumulation rate for the lake.

This parameter is essential if we are to examine bulk sedimentation and sediment contaminants in a mass balance framework. By combining the whole lake sediment accumulation rates with appropriate concentration values for sediment contaminants, we can calculate whole lake burdens of the contaminants. We can then meaningfully compare lake-to-lake differences. As well, only whole lake estimates of bulk sediment accumulation are meaningful as a measure of change in the interaction between lake and catchment area.

There were, however, several drawbacks to the work of Evans and Rigler. First, they collected no sediment cores from shallow lake depths (<10 m). As a result, they assumed

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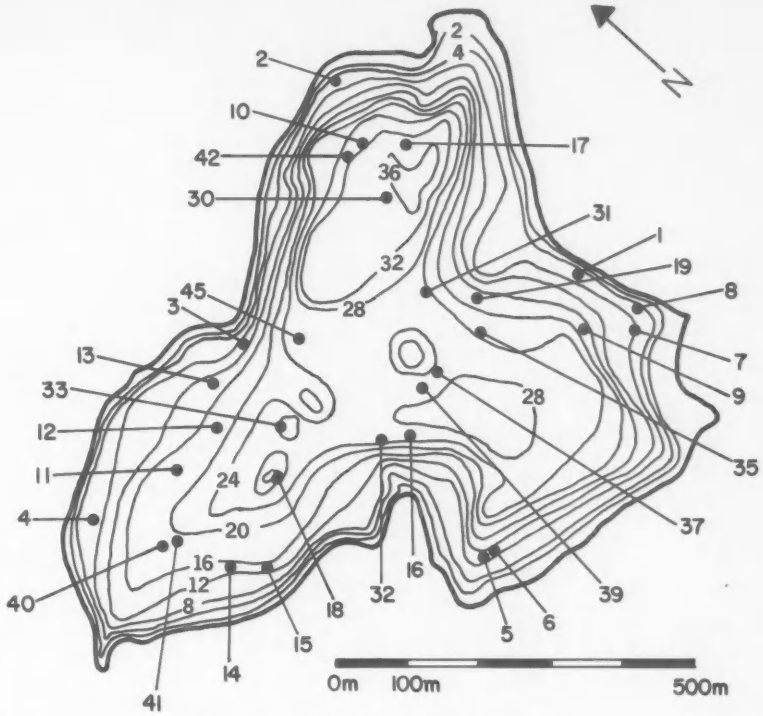

FIG. 1. Sample locations and morphometry (in metres) for Red Chalk Lake.

no sediment accumulation over the 0- to 10-m depth range which comprised 38% of the lake. Second, the study was conducted on only one lake. Thus, we have no evidence concerning the generality of their accumulation rate with depth relationship.

The aim of this work is to investigate the spatial variation in deposition of soft sediments by measuring sediment accumulation rates at a series of locations in lakes with varied morphometry and size. This would test the generality of the earlier work of Evans and Rigler and determine the feasibility of whole lake sediment accumulation as a routine limnological parameter. As well we felt that it would be instructive to look more closely at the shallow regions of lakes (those designated as erosional areas by Hakanson 1981b) to eliminate uncertainty in average lake sediment accumulation rates. As a long-term goal, it is hoped that once there are sufficient data concerning the mechanism and rates of sediment deposition in lakes, an empirical model can be developed to predict whole lake sediment accumulation quantitatively. This would eliminate much of the field work presently required.

Methods

Two lakes were chosen for this study: Costello Lake (lat. 45°35″, long. 78°20″) and Red Chalk Lake (lat. 45°11″, long. 78°56″) in southern Ontario. Both are located within 50 km of Bob Lake, studied by Evans and Rigler (1980b). About 25 sediment cores were collected from each lake (Fig. 1, 2). Core tubes of 7 cm internal diameter were used to collect the cores either manually by SCUBA diving or by using a K−B corer (Brinkhurst et al. 1969). The sediment cores were sectioned into 1- or 2-cm intervals, dried, and analyzed for ^{210}Pb activity. Lead-210 was assayed by measuring the ^{210}Po granddaughter. ^{210}Po was extracted using a modified version of the technique of Eakins and Morrison (1978; see Bloesch and Evans 1982; Evans 1980). Total stable lead was measured, after wet acid extraction of the sediment, by atomic absorption spectrometry. Total phosphorus was measured by the ignition method of Andersen (1976). More detailed information on these methods has been presented elsewhere (Evans 1980).

Results and Discussion

Sediment Accumulation in Shallow Waters

A number of cores were collected by SCUBA divers from areas of shallow water in both Costello and Red Chalk lakes. The depth at which soft sediments begin to accumulate was determined visually in both lakes by the divers. In each, the shift in sediment texture from coarse sand to soft gyttja

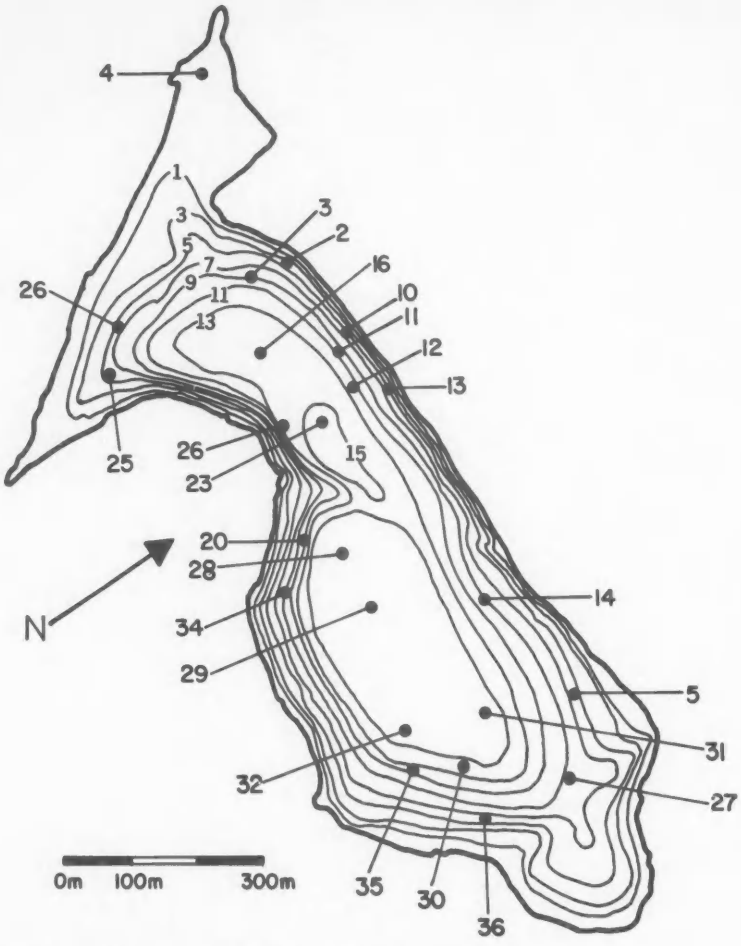

FIG. 2. Sample locations and morphometry (in metres) for Costello Lake.

occurred at water depths of 9.5–12.0 m depending on the location. At any given location, the boundary was quite distinct. An examination of water content and loss on ignition provides evidence of the fundamental shift in sediment type in this depth range. Water content is much lower per unit volume in shallows than in sediments from the center of the lakes. In Fig. 3, the water content of compacted sediments is shown as a function of lake water depth from which the sediment core was drawn. (Surficial sediments not yet compacted were not included in these calculations.) There is a distinct difference in water content above and below the transition zone. This change is also evident if one examines loss on ignition (LOI) of the surface sediments from the same cores (Fig. 4). The abrupt change in percent ignitable material occurs in conjunction with the change in water content in both lakes.

Hakanson (1981b) has discussed in great detail the mechanics of sediment deposition and erosion. He has defined areas of sediment erosion or non-accumulation as coarse sands and gravels with a surficial water content of less than 50%. Using this operational definition, the shallow regions (less than 9.5–12 m) in these two lakes would be classified as erosional areas. In Table 1, we have used Hakanson's empirical formula to predict the lake area in which sediments will be eroded or transported (A_{E+T}), i.e. areas where there is no net accumulation of soft sediments. There is good agreement between the empirical predictions of Hakanson's model and the observations of divers, although the model tends to overestimate the areas which we define as shallows. This is because it includes transportation areas as well as erosional areas. It is our feeling, based on the diver observations of the

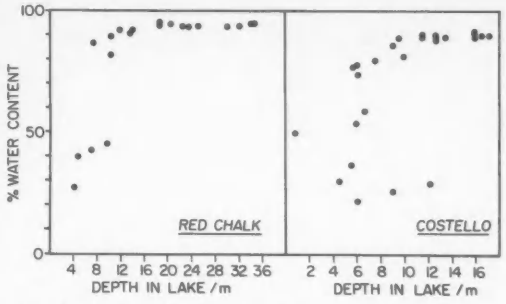

FIG. 3. Variation in water content of compacted sediments as a function of lake water depth at sample sites.

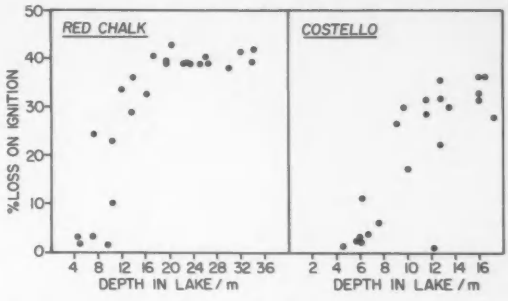

FIG. 4. Variation in % loss on ignition of surficial sediments (0–1 cm) as a function of lake water depth at sample sites.

bottom and on the predictions of Hakanson's model, that the upper boundary of recent soft sediment accumulation in Red Chalk and Costello lakes occurs between 9.5 and 12 m, and that calculations of whole lake sediment accumulation should reflect this.

These conclusions are not, however, supported by measurements of sediment accumulation using ^{210}Pb dating in these regions. Although in some cores no measurable ^{210}Pb is present, most shallow water cores exhibit typical activity versus depth profiles, similar to those found in deeper, soft sediments. Figure 5 is an example. This core (core 8) from Red Chalk Lake was taken in 4.3 m of water. Surface LOI was 2% and surface water content was 38%. The typical surface-mixed layer is followed by a good log-linear relationship of activity versus depth. (Depth is expressed in units of cumulative mass to eliminate compactive effects; see Evans and Rigler 1980b; Robbins 1978.) The only unusual aspect to the profile is the extremely low surface ^{210}Pb activity. In other cores from deep areas of the lake, typical surface activities range from 50 to 180 dpm/g dry mass. When the accumulation rate is calculated for this core, the result is 631 $g \cdot m^{-2} \cdot yr^{-1}$. This is over four times the maximum rate observed in the center of the lake. The high accumulation is primarily a function of the extremely low water content of the material in these regions.

There are two possible conclusions from these results. First, if the ^{210}Pb dating is correct, massive amounts of sandy–gravely material are accumulating in the shallow regions of lakes each year. Second, it is possible that the result is caused by an artifact and that ^{210}Pb dating does not give meaningful results in this type of sediment. Although it is not possible at present to eliminate either of these hypotheses, we believe that the second option is most likely correct. The flux of ^{210}Pb to the sediments was about one quarter that of deepwater sediments (0.56 $dpm \cdot cm^{-2} \cdot yr^{-1}$ vs. 2.0 $dpm \cdot cm^{-2} \cdot yr^{-1}$ at mid-lake). The lower flux suggests that ^{210}Pb does not readily associate with the large-sized particles found in the shallows, and thus the ^{210}Pb dating method is not applicable to coarse sediment types. Moreover, if the rates of accumulation measured in the shallows were correct, large quantities of large-sized material should build up in these regions. This would ultimately lead to instability, and some of this material would be washed down into the deeper areas. In the detailed investigation of the bottom deposits of numerous lakes, large particles of the shallow-water type have never been found in sediments from areas of the lake where soft gyttja accumulates (personal observation). The most probable explanation for the observed profiles is that a small quantity of fine-grained sediment accumulates in this area and is mixed down into the coarse sand by wave action. On the basis of visual observation, the quantity of soft sediment in this region is very small and probably insignificant in terms of

TABLE 1. Calculation of the percentage of the lake area subject to erosion and transport (i.e. non-accumulating areas).

Lake	Lake area (km^2)	Lake depth: Maximum (m)	Lake depth: Mean (m)	A_{E+T}[a] (%)	Soft sediment boundary: Predicted (m)	Soft sediment boundary: Observed (m)
Red Chalk	0.44	38.0	16.7	41.5	13.9	10.0
Costello	0.34	17.5	8.4	37.0	6.2	10.0
Bob	2.28	65.0	17.8	51.2	14.7	11.5[b]

[a]From Hakanson's (1981b) equation:

$$A_{E+T} = 52.0\left|\frac{\sqrt{a}}{Z_{mean}} - 0.2\right| \cdot \frac{Z_{max}}{3 \cdot Z_{mean}} \cdot \log \frac{60.6 \cdot Z_{mean}}{\sqrt{a}} + 19.3$$

where: a = lake area; Z_{max} = maximum lake depth; Z_{mean} = mean lake depth.
[b]Estimated from Evans and Rigler (1980b).

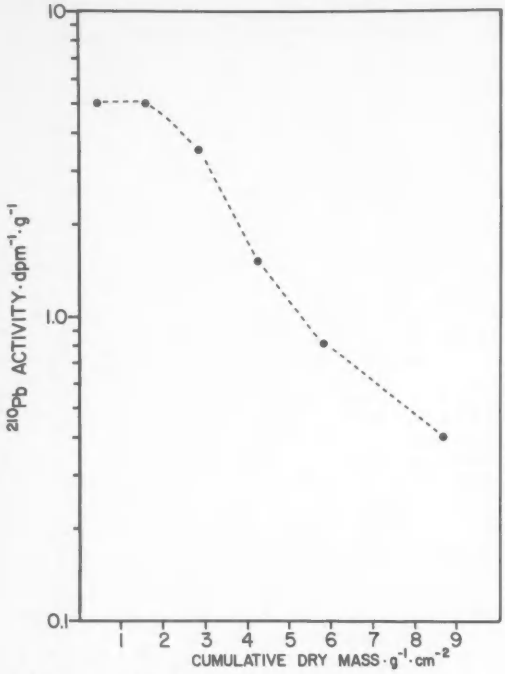

FIG. 5. Lead-210 activity profile in a shallow-water core (4.3 m) in Red Chalk Lake.

the whole lake budget of sediment accumulation. As it is not possible to reject totally the hypothesis of rapid accumulation of coarse sand, it may be more correct to refer to the calculations which follow as estimates of whole lake soft sediment accumulation.

LEAD-210 DATING AND WHOLE LAKE ACCUMULATION

Raw data for the specific activity of ^{210}Pb in each sediment core section analyzed have been presented elsewhere (Evans 1980). For each core, the sediment accumulation has been calculated in a manner similar to that outlined in Evans and Rigler (1980b).

One difference is that calculations for Bob Lake were made using only the first three or four measurements below the mixed zone. This was done because estimates of radium supported ^{210}Pb background were poor. Cores were collected from Red Chalk and Costello to obtain deeper sections and a better estimate of supported ^{210}Pb activity. Despite this, many deep water cores did not reach a stable background concentration. In those cores in which an asymptote was not reached, the lowest value for supported ^{210}Pb among the deep-water cores from a lake was used as the background activity. Sediment cores were sectioned into finer (1-cm) slices and this allowed more analyses to be included in the calculation of accumulation rates. These changes in technique allow more confidence to be placed in the results from Red Chalk and

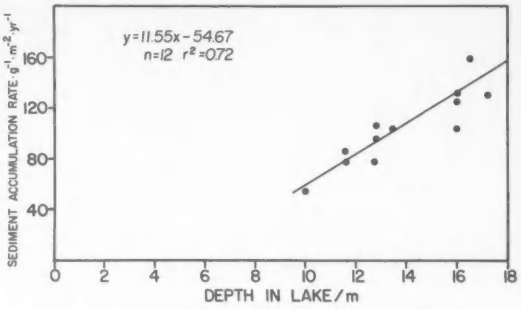

FIG. 6. Variation in bulk soft sediment accumulation rates in Costello Lake.

Costello lakes than those from Bob Lake. On average the predicted accumulation rates have an error estimate of ±10%.

One of the objectives of this work was to test the generality of the finding of Evans and Rigler (1980b) regarding the dependence of sediment accumulation rate on depth. In Bob Lake, 97% of the variance in accumulation rates was explained by water depth over the sample site. Sediment accumulation rates from various lake depths in Costello Lake are shown in Fig. 6. The relationship between accumulation and lake depth is good. Samples from the same water depth but from different areas of the lake compare well. Three samples from 12.8 m ranged between 78 g · m^{-2} · yr^{-1} and 106 g · m^{-2} · yr^{-1}. This is probably typical of variation in a shallow lake such as Costello.

To calculate the whole lake sediment accumulation, we used a regression analysis similar to that used by Evans and Rigler (1980b) in Bob Lake. Dillon and Evans (1982) have demonstrated the validity of this technique in making whole lake measurements. We assumed no fine sediment accumulation over the lake bottom where water is less than 10 m deep. All cores from areas deeper than 10 m were used in the calculation of whole lake accumulation with the exception of one core from 12 m which exhibited little change in activity with depth. It was composed of gravel and was taken from the deepest extent of the coarse, non-accumulating area. In Costello Lake the regression of sediment accumulation rate on depth explained 72% of the variation. The best fit equation of the least squares linear regression on samples taken between 10 and 17.5 m was

$$(1)\quad Y = 11.55\,X - 54.67 \quad n = 12 \quad r^2 = 0.72 \quad P < 0.01$$

The lake bottom was divided into 2-m intervals and the accumulation rate predicted by equation (1) for the midpoint of a stratum was applied over the entire 2-m interval. These calculations are detailed in Table 2. The whole lake sediment accumulation rate in Costello Lake is 47.5 g dry matter · m^{-2} · yr^{-1}.

In Red Chalk Lake, four cores taken from depths greater than 10 m exhibited uninterpretable ^{210}Pb profiles and are not included in the calculation of whole lake accumulation. Profiles from two such cores are shown in Fig. 7. The accumulation rates observed for all other cores are plotted as a func-

TABLE 2. Calculations of soft bulk sediment and sediment–phosphorus accumulation in Costello and Red Chalk lakes.

Stratum (m)	Area ($m^2 \cdot 10^{-5}$)	Midpoint accumulation ($g \cdot m^{-2} \cdot yr^{-1}$)	Total sediment accumulation ($g \cdot 10^{-5} \cdot yr^{-1}$)	Midpoint phosphorus (mg/g)	Phosphorus accumulation ($mg \cdot 10^{-5} \cdot yr^{-1}$)
			Costello Lake		
10–11	0.14	66.6	9.32	1.37	12.77
11–13	0.30	83.9	25.17	1.59	40.03
13–15	0.46	107.0	49.23	1.88	92.55
15–17.5	0.60	133.0	79.80	2.21	176.36
Totals	1.50		163.52		321.71
Lake area = $3.44 \cdot 10^5$ m^2					
Average sediment accumulation = 47.5 $g \cdot m^{-2} \cdot yr^{-1}$					
Average phosphorus accumulation = 93.5 $mg \cdot m^{-2} \cdot yr^{-1}$					
			Red Chalk Lake		
10–12	1.63	33.9	5.53	1.22	6.75
12–16	4.20	42.2	17.71	1.48	26.21
16–20	5.10	53.2	27.11	1.89	53.17
20–24	4.60	64.2	29.52	2.30	67.89
24–28	8.05	75.2	60.51	2.71	163.99
28–32	2.74	86.2	23.61	3.11	73.43
32–36	2.70	97.2	26.23	3.52	92.35
36–38	0.32	105.4	3.37	3.83	12.92
Totals	29.30		193.59		494.79
Lake area = $4.39 \cdot 10^5$ m^2					
Average sediment accumulation = 44.0 $g \cdot m^{-2} \cdot yr^{-1}$					
Average phosphorus accumulation = 112.7 $mg \cdot m^{-2} \cdot yr^{-1}$					

tion of the lake water depth at the sampling sites in Fig. 8. Although there is a strong relationship, the scatter of points is larger than that observed in either Costello or Bob lakes. Regressing accumulation rate (Y) and lake depth (X), the best fit equation was

$$(2) \quad Y = 2.75\,X + 3.67 \quad n = 17 \quad r^2 = 0.57 \quad P < 0.01$$

Only 57% of the variability in accumulation rates can be explained by depth. Part of the remaining variability may be due to the fact that the bottom topography of Red Chalk Lake is much more irregular than in Costello Lake. Kimmel (1978) suggested that bottom slope may be important in determining accumulation rate in some lakes. Moreover, a lake with a highly irregular bottom may be more prone to sediment disturbance because of locally steep areas. This could lead to erosions or slumping. Several cores from Red Chalk, especially those from depths less than 20 m, show signs of these types of disturbances, as defined by Robbins (1978), in their lead-210 profiles. (An example of this can be seen in the subsurface depression in ^{210}Pb activity in the top six sections of core 12 — Fig. 7.) These disturbances can lead to further variation as predictions of accumulation rate from cores with this type of variation are less certain than for undisturbed cores.

As in Costello, the area of the bottom over which sediments are accumulating was divided into strata and the regression equation used to predict the accumulation rate at the stratum midpoint (Table 2). Using equation (2) the predicted average accumulation in Red Chalk Lake is 45 $g \cdot m^{-2} \cdot yr^{-1}$.

PHOSPHORUS ACCUMULATION

There is no good independent test which is readily available for checking the validity of these whole lake sediment accumulation values. It would be useful to compare bulk sediment accumulation predicted from ^{210}Pb dating with that of a detailed mass balance of suspended sediment in inflows and outflow. Unfortunately, this is extremely difficult in most situations. As an alternative, Evans and Rigler (1980b) chose to test their sediment accumulation value by predicting whole lake phosphorus (P) accumulation from the bulk sediment data and comparing that value with previously measured P mass balance budgets for their study lake. To check the accumulation rates calculated for Red Chalk and Costello, phosphorus accumulation in the sediments was also determined and compared to that measured to mass balance measurements, in similar fashion to the technique used by Evans and Rigler (1980b).

In Fig. 9 and 10, the phosphorus concentrations of the 0- to 1-cm sections of the sediment cores from Red Chalk and Costello lakes are presented. There is a highly predictable relationship between phosphorus concentration and depth in each lake. As in Bob Lake, the phosphorus concentration increases towards the deepest area of the lakes. Even over the small range of depths found in Costello Lake, the change in phosphorus concentration is twofold. A possible explanation of this phenomenon is that in addition to spatial variation in the quantity of accumulating material per unit time, there is spatial variation in the quality of material accumulating. In

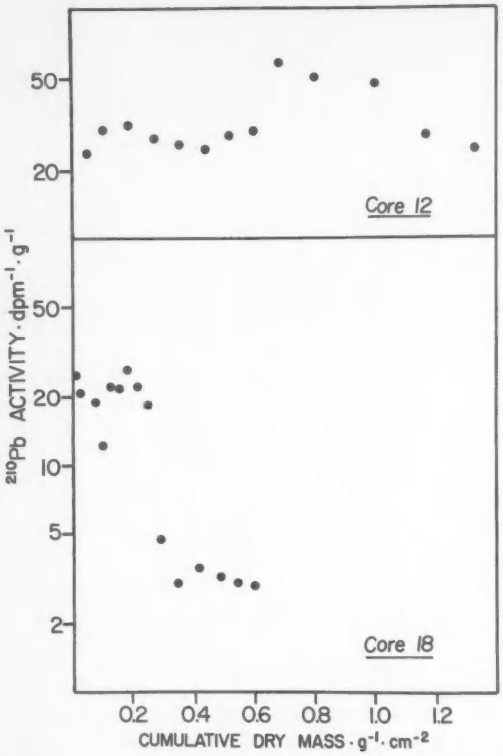

FIG. 7. Two uninterpretable ^{210}Pb profiles from Red Chalk Lake.

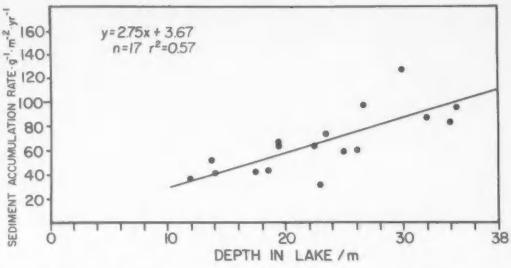

FIG. 8. Variation in bulk soft sediment accumulation rates in Red Chalk Lake.

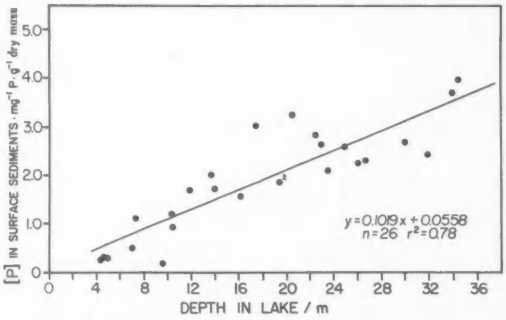

FIG. 9. Surficial (0–1 cm) sediment phosphorus concentrations in Costello Lake.

other words, there may be a shift in the type of material accumulating over the 10- to 17.5-m range.

It has been suggested by Carignan and Flett (1981) that postdepositional mobility of P in sediments can alter profiles. To determine whether surficial P concentrations in Red Chalk and Costello are representative of recent material, complete profiles for three cores were analyzed from shallow, mid, and deep locations in each lake. Phosphorus profiles from cores 32 and 35 in Costello Lake are similar to those found in Bob Lake in that there is an increase in P concentration with depth into the core (Fig. 11). Core 34 from 9.1 m, which is the shallowest of the three, exhibits an increase in concentration towards the surface. Although it is perhaps tempting to assume that this increase is due to diagenetic movement, this hypothesis cannot explain the increase in concentration at lower depths in the core.

Similar fluctuations in concentrations are found in Red Chalk profiles (Fig. 12). There is no consistent pattern in the variation in P concentrations. In view of the variability in profiles within each lake, and in the absence of a theory which could explain them otherwise, we have assumed that the phosphorus concentrations and therefore the concentration of P in the 0- to 1-cm section of a sediment core is appropriate to the calculation of P retention. This view is supported in some measure by the predictability of the surficial P concentrations across the lake bottom.

An alternate method of determining the appropriate concentration of phosphorus in sedimenting material for P retention calculations is to collect the falling seston in sediment traps. This was done on three occasions during the stratified seasons in Red Chalk Lake in 1976 (Evans and Dillon unpublished data). Sediment was collected in traps suspended below the thermocline and located in the middle of the lake. The traps were negatively buoyant acrylic tubes, 10 cm in diameter and ~60 cm long, suspended from subsurface floats. This design has been shown to collect falling sediment efficiently in small, calm lakes like Red Chalk (Bloesch and Burns 1980). The average P concentration of five samples collected over three 2-wk periods was 2.4 mg P/g dry seston, suggesting that the use of surficial P concentrations is appropriate.

To obtain the P retention, a least squares linear regression equation was fit to the phosphorus and lake water depth data. The regression for each lake was used to predict the phosphorus concentrations at the midpoint of each stratum used in the whole lake sediment accumulation calculations. These values were combined with bulk accumulation data to calculate phosphorus storage in the sediments (Table 2). Phosphorus retained in the sediments of Costello Lake is 93.5 mg · m^{-2} · yr^{-1}. In Red Chalk Lake sediment P storage is 113 mg · m^{-2} · yr^{-1}.

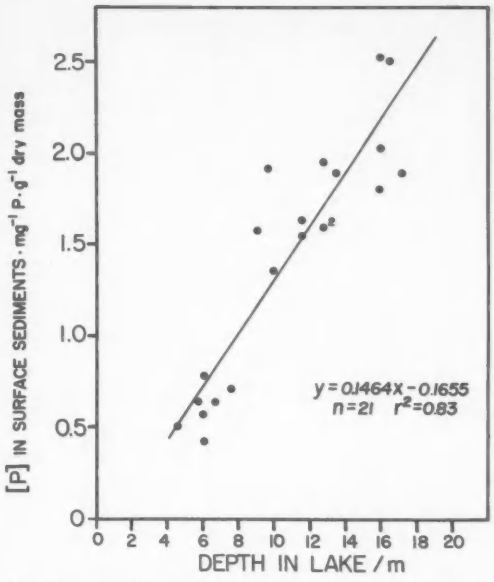

FIG. 10. Surficial (0–1 cm) sediment phosphorus concentrations in Red Chalk Lake.

Scheider (1974) has determined the retention of phosphorus in Costello Lake as the difference between measured inputs and outputs. He found the mass of P retained by the lake to be 86.5 $mg \cdot m^{-2} \cdot yr^{-1}$. This is quite comparable to the 95 $mg \cdot m^{-2} \cdot yr^{-1}$ determined by the sediment accumulation method. If one is realistic about the potential errors associated with each method, the two estimates are not significantly different. Thus we believe that the measurement of whole lake sediment accumulation of 48 $g \cdot m^{-2} \cdot yr^{-1}$ in Costello is quite accurate.

The input and output of phosphorus in Red Chalk Lake has been measured for 4 yr (June 1976–May 1980; Dillon and Scheider unpublished data). The annual P retention has averaged 69 $mg \cdot m^{-2} \cdot yr^{-1}$ (range of 49–96 $mg \cdot m^{-2} \cdot yr^{-1}$). However, this retention is the combined value for Red Chalk Lake and the lake immediately upstream, Red Chalk East. The value for Red Chalk Lake alone may not be exactly the same. As there is some uncertainty about the mass of phosphorus input to the main lake and hence the actual retention, it is possible to predict a retention by rearranging the mass balance model developed by Dillon and Rigler (1974) such that:

$$(3) \quad R_p = P \cdot Q \cdot R / A(1 - R) \quad (\text{in } mg \cdot m^{-2} \cdot yr^{-1})$$

where: A = lake area (in m^2)
Q = outflow water discharge (in $m^3 \cdot yr^{-1}$)
P = lake phosphorus concentration (in $mg \cdot m^{-3}$)
R = fraction of input mass of P retained by lake.

This model assumes no knowledge of the input of phosphorus to the lake except indirectly through the lake P concentration.

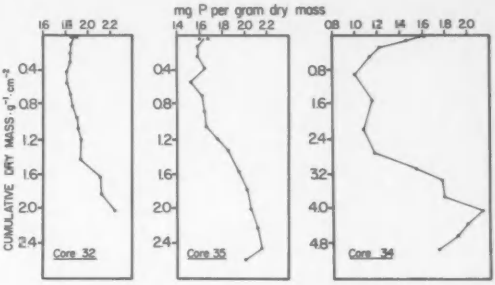

FIG. 11. Sediment–phosphorus profiles from three Costello Lake cores. Depth is expressed as cumulative mass per unit area.

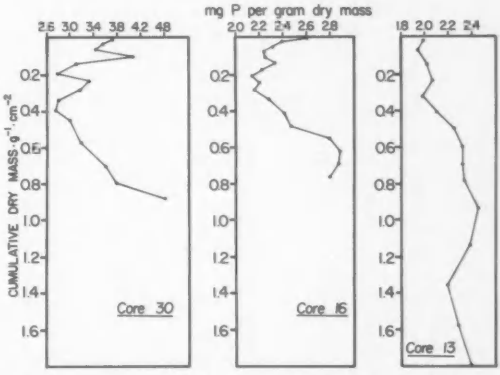

FIG. 12. Sediment–phosphorus profiles from three Red Chalk Lake cores. Depth is expressed as cumulative mass per unit area.

This technique of estimating P retention has been used by Cornett and Rigler (1979). Using values for P, Q, and R of 5.6 $\mu g \cdot L^{-1}$, $3.29 \cdot 10^6$ $m^3 \cdot yr^{-1}$ (Scheider unpublished data), and 0.68 (Ostrofsky 1978), respectively, this model predicts a phosphorus retention for Red Chalk Lake of 90 $mg \cdot m^{-2} \cdot yr^{-1}$. There is a larger difference between P retention and sediment storage of P in Red Chalk than in the other two lakes. This may indicate that the estimate of bulk sediment accumulation in Red Chalk Lake is somewhat high.

In each of the study lakes (Evans and Rigler 1980), the concentration of phosphorus in surficial sediment (0–2 cm) varied as a function of depth, with highest concentrations in the deepest areas of the lake. A similar observation was recorded in Bob Lake by Evans and Rigler (1980b). This phenomenon has also been reported in Lake Esrom by Kamp-Nielsen and Hargrave (1978), who interpreted it as evidence of sediment focusing. This is a misinterpretation. Changes in concentration of an element reveal nothing about changes in sediment accumulation rates which are changes in mass accumulating per unit time.

The type of material found in the sediments of deep areas is higher in both phosphorus and nitrogen (Kamp-Nielsen and Hargrave 1978). There is evidence of a slight increase in LOI in Red Chalk and Costello (Fig. 2) in soft sediments with

increasing water depth, which would indicate an increase in organic matter content. The most probable mechanism to account for these concentration variations is one of selective particle-size distribution. Yuretich (1979) and Thomas et al. (1972) have measured variation in particle-size distribution over lake bottoms. Both found that particle size decreases with increasing water depth. If these results can be extrapolated to Red Chalk and Costello lakes, it might be hypothesized that as particle size decreases, binding capacity for nutrients such as P and N increases. Such a mechanism has been demonstrated clearly for binding capacity of trace metals on particles (Forstner and Salomons 1980). Whatever the mechanism that causes this variation in nutrient concentration, it is apparent that if one desires to quantify sediment phosphorus retention, spatial variation in both bulk accumulation rates and phosphorus concentrations over a lake bottom must be measured.

There is little difference in the whole lake sediment accumulation for the three lakes for which data now exist. It is difficult to tell, with this small a data set, whether an approximation can be made for small Laurentian Shield lakes. There does not appear to be, as might be expected, any relationship between the size of the catchment area and the whole lake sediment accumulation. Although the results of whole lake accumulation calculations support the contentions made by Evans and Rigler (1980) that ^{210}Pb dating can be used in a variety of small lakes and that variation in sediment accumulation rates is related to changes in lake bottom depth, there are several areas which require further study. First, the upper limit of accumulating sediment is not certain. Although it can be established visually, a predictive model for this parameter such as Hakanson's (1981b) is more useful. This model should be tested further to examine its validity in small lakes. In addition, as there is variation in the depth of this transition, some error is introduced by the arbitrary fixation of a depth for calculating whole lake accumulation. The reason for the extremely high accumulation rates predicted by ^{210}Pb dating in shallow areas of no apparent accumulation requires further study. Lead-210 dating in general requires much further work in as wide a variety of situations as possible. There is still an element of subjectivity required in the choosing of data points to be used in an accumulation calculation. No one to date has presented an unambiguous method for rejecting anomalous data points. In addition, in some lakes at least, dating by ^{210}Pb is confounded by disturbances.

The results of ^{210}Pb dating in Costello and Red Chalk lakes and the comparison of phosphorus retentions to mass balances support the hypotheses put forward. Morphometry strongly influences the variation in sediment accumulation across the bottom of a lake. The relationship of this variation to morphometry can be utilized to simplify measurement of whole lake sediment accumulation. These results suggest that ^{210}Pb dating of a series of sediment cores in a lake will provide meaningful and useful measurements in small temperate lakes.

Acknowledgments

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An Investigation of the Relationship Between Oregon Coho Salmon (*Oncorhynchus kisutch*) Hatchery Releases and Adult Production Utilizing Law of the Minimum Regression

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CLARK, J. AND B. MCCARL. 1983. An investigation of the relationship between Oregon coho salmon (*Oncorhynchus kisutch*) hatchery releases and adult production utilizing law of the minimum regression. Can. J. Fish. Aquat. Sci. 40: 516–523.

This study examines aggregate relationships between coho salmon (*Oncorhynchus kisutch*) adult production and hatchery releases within the Oregon Index Area (OIA). Previous analyses have indicated the presence of density dependence, and concluded with a request for a reduction in hatchery smolt releases. The hypothesis that density dependence is exhibited in the OIA is tested via a broad correlation approach. Several regression models are used including one unique one in fisheries research based on limiting factors.

Analysis was done on the fitted regression equations including a simple simulation of release policies. Neither significant density dependence nor a statistically supportable technical maximum for smolt releases was found. The limiting factors regression technique generally gives the best results of all the models employed, and thus appears potentially useful in this type of fisheries work.

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On trouvera dans ce qui suit une analyse des relations globales entre la production de saumons coho (*Oncorhynchus kisutch*) adultes et les peuplements de poissons d'élevage dans l'*Oregon Index Area* (OIA). Des analyses antérieures ont indiqué une dépendance de la densité, ce qui a conduit à demander une réduction des peuplements de smolts d'élevage. L'hypothèse d'une dépendance de la densité dans l'OIA a été vérifiée dans une approche de corrélations globales. Plusieurs modèles ont été utilisés, y compris un modèle fondé sur les facteurs limitants, unique en recherche halieutique.

Une analyse des équations de régression ajustée, incluant une simulation simple des politiques de peuplements, a été effectuée. Nous n'avons trouvé aucune dépendance de la densité non plus qu'un maximum technique statistiquement défendable de peuplements de smolts. De tous les modèles utilisés, celui de la régression des facteurs limitants a généralement donné les meilleurs résultats et semble prometteur dans ce type de recherche.

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SALMON stocks of the northeast Pacific Ocean are and have been an important resource. Recently, man has increasingly felt the need to be actively involved in maintenance and enhancement of these stocks. However, a significant obstacle exists to the careful formulation of current and future maintenance and enhancement plans. Namely, the efficacy of the schemes which have been and/or could be carried out is highly uncertain.

Currently, salmon management is of widespread interest, particularly as there are some salmon fisheries which, on cursory examination of performance data, appear to be exhibiting negative returns to enhancement efforts. Such behavior is potentially illustrated by the coho salmon (*Oncorhynchus kisutch*) fishery in the Oregon Index Area (OIA), as measured by the Oregon Production Index (OPI). The characteristics of these data are discussed below.

Figure 1 is a plot of the relationship between the number of adults attributed to nonprivate hatcheries (McGie 1980) within the OPI and nonprivate hatchery smolt releases (lagged 1 yr) for 1961–79. The data are not inconsistent with a belief that hatchery releases exhibit density dependence, but perhaps more importantly, with a belief that increases in releases lead to a decrease in total production and that the low returns in the years following the highest releases could imply that too many smolts are currently being released.

Various models have been used in the past to explore the density dependence question. The simplest class includes those models which ignore other factors considering the number of adult salmon in the fishery (A) to be a function of number of smolts (S) only. Models of this type were used by,

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for example, Peterman (1978, 1981) and Ricker (1976).

These simple models incorporate the assumption that the factors which affect salmon survival, apart from the number of smolts, are constant from year to year. However, systematic variation in these other factors could easily bias the statistical results, altering the likelihood that the estimation results would or would not exhibit density dependence. A number of studies have been done which attempt to account for factors which affect salmon survival. For example, Peterman and Gatto (1978) investigated predation as it impacts returns for pink and chum salmon. Walters et al. (1978) examined zooplankton distribution, ration and growth for juveniles, mortality and body size, and timing and ocean position in a rather complex simulation model for salmon species entering the Pacific Ocean from British Columbia streams. Ricker (1975, 1976) reviews numerous factors which are linked to survival. Mathews and Olsen (1980) examine releases and summer stream flow. The Oregon Department of Fish and Wildlife, through a number of studies, examined among other issues the impact of releases and upwelling (Gonsolus 1978; McGie 1980, 1981; ODFW 1982).

The studies specifically dealing with the salmon stock represented by the OPI have not consistently arrived at the same conclusion. McGie (1981) concludes that the depressed levels of abundance are primarily the result of density dependent mortality and low upwelling. Further, McGie suggests reductions in smolt releases. The 1982 ODFW Coho Plan presents two appendices, one which supports the existence of density dependence, and one which rejects it. Peterman (1981) also studied this question finding "no statistical evidence of density dependent marine survival" (p. 1118). Thus, one purpose of this study is to attempt to estimate the relationship between smolt releases, environmental variables, and adult production. In turn, the results of our analysis will be used to simulate the forecasted effects of releases on the OPI.

Estimation of output response to changes in the level of inputs is frequently done within fisheries (i.e. Ricker 1975) and agriculture (Dillon 1976). One model of response, which has received recent attention in agriculture, arises from Liebig's (1862) concept of limiting factors (Perrin 1976; Cate et al. 1978; Lanzer and Paris 1981). Liebig postulated that the level of crop production is determined by the most limiting chemical element available. This proposition is commonly called the law of the minimum. Recently, Hartley et al. (1978) developed a technique which allows one to estimate the underlying limiting factors relationships. The law of the minimum proposition potentially can be applied to the fishery. Thus, the second and principal purpose of this paper involves the utilization of the law of the minimum concept in the attempt to determine the existence of density dependent mortality in the OIA, and a comparison of the law of the minimum results with ordinary regression results.

Data and Development of Estimating Equations

The basic methodology of this study involves estimation of models explaining the share of the OPI (in units of thousands adult cohos) attributed to hatcheries (OPIAH) as a function of lagged releases (in units of millions of smolts) and lagged upwelling [portrayed by a weighted average of the NOAA

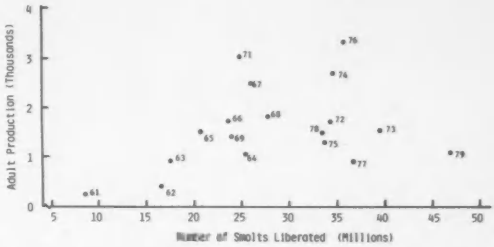

FIG. 1. Relationship between coho salmon production and hatchery coho salmon smolts lagged 1 yr.

upwelling indices (Bakun 1973) as explained by Gonsolus]. The data used are rather aggregate. The OPI is an index of coho abundance representing the number of adults harvested in one form or another south of Ilwaco, WA. The OPI is used directly in the management of the coho stock by both Oregon and the Pacific Fisheries Management Council. Its specific characteristics are discussed in the Oregon Department of Fish and Wildlife's (ODFW) Coho Salmon Plan (ODFW 1982). The OPIAH is an adjusted OPI to account for hatchery releases excluding wild fish. The data were drawn directly from McGie (1980), who explains the adjustment process. These data abstract from many potentially important factors such as diet, rearing conditions, time of release, place of release, genetic diversity, freshwater conditions, etc. The omission of these factors might bias estimation results. For example, a decrease over time in smolt quality could, when coupled with increased releases, lead one to identify mistakenly density dependency. This possibility was investigated in the Coho Plan (1982). The results suggest that a small proportion of the variation in adult production in the OPI could be explained in this manner. It does not appear, however, that the effect is large enough to alter significantly the results of the aggregate analysis used in this paper. In spite of the limitations associated with the aggregate nature of the analysis, we are using these data because of the ongoing policy debate regarding them (as illustrated by appendices *f* and *g* in the 1982 ODFW report), because other efforts have used the same data for the same purpose (Gonsolus 1978; McGie 1980, 1981; Peterman 1981), because the data allowed us to fulfill our methodological objectives, and because of a lack of better data.

The models explaining the OPIAH will be estimated utilizing regression techniques. The functional forms used (given explicitly in Table 1 below) are a simple quadratic in releases only [which is quite commonly used in agricultural response work (Dillon 1976)]; a Ricker curve involving releases only (Ricker 1976); a simple linear model using upwelling and releases (following McGie 1980, 1981); a modified Ricker curve in which the exponent term incorporates both upwelling and releases (following ODFW Coho Plan, Appendix *f*), and a model based on the law of the minimum concept. All of the models except the law of the minimum are estimated by ordinary least squares. The law of the minimum model, however, is estimated via a different technique and merits discussion.

The law of the minimum estimation technique embodies the concept that the output variable is constrained by several

TABLE 1. Results for regressions of OPI production (A_t) in year t on the previous years ($t-1$) ocean upwelling (U_{t-1}) and previous years releases (R_{t-1}) using five different regression models.[a,b]

Equation 1: Returns a quadratic function of releases only

Functional form: $A_t = b_0 + b_1 S_{t-1} + b_2 S_{t-1}^2$

Estimation results

Parameters	b_0	b_1	b_2
Estimates	−1992	246.7*	3.89
Standard errors	1175	8.63	1.53
Coefficient of determination (R^2)	0.37	Adjusted	0.30[c]

Equation 2: Ricker curve

Functional form: $A_t = b_0 S_{t-1} e^{b_1 S_{t-1}}$

Estimation results

Parameters	b_0	b_1
Estimates	60.081*	−0.00549
Standard errors	—[d]	0.01303
Coefficient of determination (R^2)	0.28	Adjusted 0.19

Equation 3: Returns a simple function of releases and upwelling

Functional form: $A_t = b_0 + b_1 S_{t-1} + b_2 U_{t-1}$

Estimation results

Parameters	b_0	b_1	b_2
Estimates	−463	24.4	5.28*
Standard errors	592	16.3	1.50
Coefficient of determination (R^2)	0.50	Adjusted	0.44

Equation 4: Law of minimum

Functional form: A_t = minimum of $(b_0 + b_1 S_{t-1}; d_0 + d_1 U_{t-1})$

Estimation results

Parameters	b_0	b_1	d_0	d_1
Estimates	−766.25	115.5*	−519.98	9.75*
Standard error[e]	—	—	—	—
Coefficient of determination (R^2)	0.66	Adjusted	0.59	

Equation 5: Modified Ricker curve

Functional form: $A_t = b_0 S_{t-1} e^{b_1 S_{t-1} + b_2 U_{t-1}}$

Estimation results

Parameters	b_0	b_1	b_2
Estimates	26.546	−0.01059	0.00366*
Standard errors	—[f]	0.00918	0.000844
Coefficient of determination (R^2)	0.57	Adjusted	0.51

[a]Recruitment (A) is in units of 1000 fish, releases (S) is in units of 1 000 000 smolts, and upwelling (U) is depicted by an index.

[b]An * denotes a coefficient significantly different from zero at the 5% level.

[c]This is the coefficient of determination adjusted for degrees of freedom.

[d]This coefficient yielded a t of 4.62 in logarithms.

[e]The standard error on the law of the minimum equation has not been derived. We did run OLS estimates on the laws and the observations they uniquely explained (law 1 explained 7 observations, law 2 explained 12 observations). This revealed the slopes to be significantly different from zero.

[f]This coefficient yielded a t of 2.93 in logarithms.

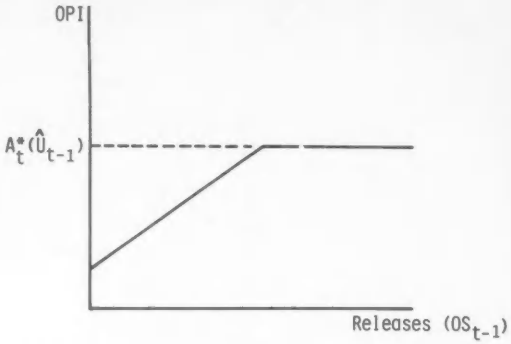

FIG. 2. A graph of the law of the minimum relationships explaining output for the coho fishery given an observed level of upwelling.

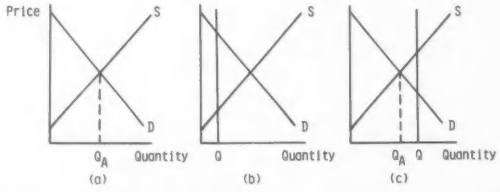

FIG. 3. Economic markets which are (a) in equilibrium, (b) in disequilibrium because of a binding quota, and (c) in equilibrium with a non-binding quota.

limiting factors. The exact level of the output variable is explained by the most limiting factor. In the OPI estimation below, the OPI (A_t) is assumed to be constrained by two explanatory factors, lagged upwelling, a proxy for ocean food supply when the smolts first reach the ocean (depicted as U), and smolt releases (depicted as S_{t-1}). The explanatory relationship assumes a 1-yr lag between these variables and output to account for the life cycle characteristics of the coho.

$$A_t = \min \begin{cases} b_o + b_1 S_{t-1} \\ d_o + d_1 U_{t-1} \end{cases}.$$

This assumes a linear relationship between output and each factor until the maximum amount of output supported by the other factor is reached. An example of this process is given in Fig. 2. Assume that upwelling in a year ($t-1$) is U_{t-1}; then the associated output forecast by the upwelling equation is $A_t^*(U_{t-1})$. The OPI observed then will be that explained by releases up until the point at which the OPI forecast due to releases equals that due to upwelling. Beyond that any increase in releases does not increase the OPI.

This procedure, although apparently new in fisheries, historically has arisen in two contexts: crop response to fertilizer and economic markets in disequilibrium. The concept arose in the fertilizer context with Liebig (1862). Recently, this concept has received considerable attention (e.g. Waugh et al. 1973, 1975; Perrin 1976; Cate et al. 1978; Lanzer et al. 1979; Lanzer and Paris 1981). Numerous estimation methods have been applied in these studies including spline regression

TABLE 2. Predictions of OPIAH production standard deviation and coefficient of variation for alternative release policies from the modified Ricker and law of the minimum models.

Releases policy	A_r[a]	σ_r[b]	A_{LM}[a]	σ_{LM}[b]	CV_{LM}[c]
(10^6 smolts)	(10^3 fish)	(10^3 fish)	(10^3 fish)	(10^3 fish)	
5	355	124	189	0	0
10	673	236	389	0	0
15	958	336	928	118	0.13
20	1212	425	1370	302	0.22
25	1436	504	1672	518	0.31
30	1635	573	1903	742	0.39
35	1809	634	2056	918	0.45
40	1961	686	2075	945	0.46
45	2092	734	2075	945	0.46
50	2205	773	2075	945	0.46
55	2300	806	2075	945	0.46
60	2380	834	2075	945	0.46
65	2445	857	2075	945	0.46
70	2497	876	2075	945	0.46
75	2538	890	2075	945	0.46
80	2567	900	2075	945	0.46
85	2587	907	2075	945	0.46
90	2598	911	2075	945	0.46
94.4	2600	912	2075	945	0.46

[a] A_r, A_{LM} are the output predictions from, respectively, the Ricker and law of the minimum equations.

[b] σ_r, σ_{LM} are the standard deviations of output from, respectively, the Ricker and law of the minimum equations.

[c] CV_{LM} is the coefficient of variation of output from the law of the minimum equation. The coefficient of variation for the Ricker curve is 0.35 at all release policies.

(Lanzer and Paris 1981), nonlinear regression (Waggoner and Norvell 1979), variational analysis with filtering constraints (Cate et al. 1978 — based on Wagner 1971), and a form of maximum likelihood estimation (Lanzer et al. 1979).

The concept also arose in terms of economic models in disequilibrium. The basic application of the concept is best shown graphically (Fig. 3). An ordinary supply and demand system will equilibrate where supply and demand are equal (point Q_A, Fig. 3a). However, if a binding quota (line Q in Fig. 3b) is imposed, then the market will not equilibrate but rather the quantity traded will equal the quota. But, the quota may be larger than the equilibrium quantity, in which case the market will equilibrate at the intersection of supply (S) and demand (D) (Fig. 3c). Thus, the quantity traded is the minimum of the quota or the equilibrating quantity. This is standard fare in economics (arising in Hicks 1939). Recently, however, starting with Fair and Jaffe (1972), substantial interest has arisen in both the theory and estimation of such systems (e.g. Hartley 1976, 1977; Hartley and Mallela 1977; R. Quandt, Dep. of Economics, Princeton University, Princeton, NJ, 1979, unpublished data; Chambers et al. 1981a, b). Estimation of these equations (a special case of law of the minimum with the number of factors equal to two) has mainly been done through maximum likelihood procedures (e.g. Fair and Jaffe 1972; Hartley 1977).

These two approaches were brought together in 1978 by Hartley, Hartley, and Bowen (HHB). They developed a maximum likelihood estimator for the N factor case. This estimator is used here and is reviewed below.

HARTLEY, HARTLEY, AND BOWEN'S LAW OF MINIMUM ESTIMATOR

The law of the minimum postulates that output (Q) is determined by the minimum of a number of explanatory factors which in turn are a function of a number of underlying independent variables. Mathematically

$$Q_K = \min_i G_{iK} \quad \text{where } G_{iK} = f_i(X_{iK})$$

where Q_K is the Kth output observation, G_{iK} is the ith factor function equaling $f_i(X_{iK})$. The functions $f_i(X_{iK})$ involve underlying independent variables (X_{iK}) potentially explaining the Kth output observation. The Kth output observation (Q_K) is then chosen as the minimum of the various explanatory factor predictions.

Hartley, Hartley, and Bowen (HHB) formulated a model in which the laws G_i were linear functions of the explanatory variables (X_i);

$$G_{iK} = X_{iK}\beta_i.$$

However, the prediction of the Kth observation on Q is determined by the minimum of the prediction from the various laws evaluated at the independent variable values associated with that observation;

$$Q_K = \min_i G_{iK} = \min_i X_{iK}\beta_i.$$

HHB derive a maximum likelihood estimator for determining the estimates of the parameters (β) and the variance (σ^2). The maximum likelihood estimator function is determined as follows: assuming that the error terms are normally distributed, the probability of an output (Q_K) exceeding a given level (Q_K) is the joint probability that all laws simultaneously exceed that level. Thus, HHB formed the cumulative density function relative to the estimation. Differentiating this function and taking the natural logarithm leads to a log-likelihood function which is then differentiated to obtain equations from which an estimate of β is obtained.[1] HHB's estimation equation for β is:

$$\beta = (X'WX)^{-1}X'WQ$$

where W is a matrix of weights (not unlike those used in generalized least squares). However, the W's are functions of the X's so a nonlinear iterative estimation procedure is called for.

The same approach is used for the estimate of variance. However, HHB point out that the expression is relatively cumbersome and therefore they chose to use finite difference formulas to obtain approximate solutions. More details on the implementation of the above algorithm and a simplified example are provided in the appendix.

Estimation Results

Not all the functions explained the data equally well. Equation 4 (or more properly equations) is the law of the minimum estimate and explains 66% of the variation in the data. Equation 5 is the modified Ricker and explains 57% of the variation in the data. This equation exhibits a shape consistent with density dependence. However, upwelling is the only statistically significant factor. Equation 1 is a simple quadratic function. The shape is consistent with density dependence. Similarly, equation 2 — the Ricker curve — also possesses a shape consistent with density dependence. Estimates by the quadratic function (equation 1) and the Ricker curve (equation 2) fit the data rather poorly, explaining only 37 and 28%, respectively, of the variation in the data. In addition, equation 3, a model which considers the impact of upwelling, explains more of the variation (50%) with both upwelling and releases positively contributing to output. However, the regression coefficient for releases is not significantly different from zero, whereas the upwelling coefficient is, pointing out the importance of considering upwelling.

The results indicate several things. First, upwelling is an important factor in prediction and was significant in all equations that it entered. Thus, the impact of releases should not be deduced from an analysis as implicit in Fig. 1 or equations 1 and 2; rather, other factors need to be considered. Thus, statistical analysis which is undertaken to determine density-dependence, which is concerned only with adult production and releases, is very likely to be incorrect. The statistical pattern with respect to the OPI during the 1960s and 1970s is a case in point. Smolt releases increased throughout the period. Adult production first increased and then decreased, exhibiting classic density dependence. On the other hand, the upwelling index was much higher in the 1960s than the 1970s, which accounts for much of the decline in adult production in the 1970s.

Second, the functions which could exhibit a density-dependent shape did (equations 1, 2, 5). However, the parameters which make the equation exhibit density-dependence are not statistically significantly different from zero (i.e. b_2 in equation 1, b_1 in equations 2 and 5).

Finally, equations 4 and 5 seem to provide the best explanations of the data, but they don't explain a considerable amount of the variation. Thus, more work is necessary which involves other factors such as stream conditions, smolt characteristics, release locations, or expanded data on ocean conditions.

Evaluation — The Law of the Minimum

The law of the minimum estimator (LOME) performed well on simple Monte Carlo experiments in seeking out underlying causal relationships (see appendix). When applied to the OPIAH data, a model (equation(s) 4) was produced which is generally superior to any regression model we found, and is much simpler. Our investigations utilizing this method, however, turned up a number of factors to consider.

First, the method is by nature a nonlinear estimator technique working over a potentially nonconvex region. Thus, local optimals are possible. This did not trouble us in working with the linear equations. We did try some nonlinear functions and obtained different parameter estimates when starting from different starting points.

Second, the method did not work well when we entered two fairly good explanatory factor functions. This led to two different types of results. First, when running two equations, one against the other in which additional variables were included to an earlier equation, the unadjusted coefficient of determination declined. For example, adding the variable S^2 to the law of the minimum first equation above led to a coefficient of determination equaling 0.5 with equation 1 eliminating equation 2 statistically. This type of result was unexpected as we were accustomed to the notion that adding independent variables always increases the unadjusted coefficient of determination. Second, when running a good nonlinear equation against another equation, the nonlinear technique left the parameter estimates unchanged from the starting solution.

Third, the method, to a large degree, simply partitions the data into a number of subsets, each explained by a different equation. Thus, in some cases we were able to duplicate the LOME results by ordinary regression estimation after the fact, using the relevant data subsets for each equation. However, this did not always work. In some cases both equations estimated observations equally well and this altered the estimates.

Fourth, HHB did not derive an estimate of the standard error of the coefficients, nor did we. This is desirable and likely possible, although it appears analytically difficult. As

[1]The algebra involved in deriving this estimator is relatively involved and unfortunately unpublished except in the Ph.D. thesis of Bowen (1979). We have chosen not to reproduce it in full here, but are prepared to supply the HHB version and the computer implementation at cost to interested parties. Those interested should contact Dr Bruce McCarl.

alluded to above, regression can be used to obtain some idea of coefficient significance. However, such standard deviation estimates are biased.

Finally, the law of the minimum estimator appears to be potentially useful in fisheries work as it allows one to estimate the nature of underlying causal factors.

Implications of Results

An important management issue is the maximum number of smolts to release. This cannot be fully determined here because of several factors. The limited data base, the possibility of important missing data, incomplete model explanations, and statistically insignificant smolt release terms limit the reliability of such answers. However, given even perfect data, the question of "optimal" releases would require information on future upwelling, the economic value of adults, and the costs of releases. Given these data, then the economic optimal level of releases would be calculated so that the optimal benefits minus costs would be obtained. This is not possible within this paper because of a lack of information of the costs and benefits. However, with this disclaimer we present a tentative evaluation of the number of smolts released which results in the physical maximum OPI.

The technical maximum is for: (a) equation 1, 31 700 000 smolts; (b) equation 2, 183 149 000 smolts; (c) equation 3, no maximum; (d) equation(s) 4, no maximum, and (e) equation 5, 94 400 000. Equation 3 is linear with respect to smolts and with a positive estimated coefficient there is no technical maximum. For the law of the minimum, as the index of upwelling increases, so does the maximum for smolt releases. However, for any given level of upwelling there is an identifiable maximum for smolt releases. This characteristic of the law of the minimum will be explored below. The maximum releases and the results of the maximum release policies vary substantially, Therefore, we decided to investigate the impact of fixed release policies on output and its variability (Table 2). Assuming no a priori knowledge of upwelling, the law of the minimum results indicate that releases in excess of 40 million smolts are wasted, whereas the modified Ricker results show that although smolt releases increase OPIAH until 94.4 million smolts output, only a 25% gain in output is obtained by more than doubling smolts released from the 45 million level. In addition, the coefficient of variation is substantial, indicating that (assuming normality) at a continuing release policy of 40 million, a 90% confidence interval for releases spans from 832 thousand adult coho to 3.09 million for the modified Ricker curve and between 520 thousand and 3.63 million for the law of the minimum.

Summarizing, it appears that a conclusion about release policy is uncalled for. We cannot conclude firmly what maximum releases should be, although the range appears to run from as small as 32 million to as large as around 180 million.

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Appendix A

IMPLEMENTATION OF THE ESTIMATOR

Bowen (1979) constructed a computer program implementing the HHB procedure. Bowen's implementation involves a nonlinear iterative procedure which proceeds as follows:

Step (1). Develop initial estimates of β and σ^2 by regressing each law independently on the data.

Step (2). Given the prior estimate of β and σ^2, revise the estimate by application of the formulas derived from the maximum likelihood procedure.

Step (3). Test for convergence of β and σ^2 estimates. If convergence is not obtained, go to Step (2), otherwise go to Step (4).

Step (4). Test to see whether any of the laws can be eliminated by:

a) seeing if any laws fail to contribute to the explanation of the output level (i.e. eliminate those laws which are never the minimum on any observation);

b) seeing if any laws fail to contribute significantly (this

TABLE A-1. Law of the minimum results.[a]

	Bodies			Wheels			Order			Random			
Interaction	β_0	β_1	σ	β_0	β_1	σ	β_0	β_1	σ	β_0	β_1	σ	Log of likelihood
0	2.450	0.562	8.30	2.808	0.141	9.00	18.102	−0.116	11.00	15.494	0.011	11.06	—
1	1.885	1.579	5.57	1.039	0.470	6.11	61.357	−0.309	9.18	15.494	0.011	10.28	−135
2	0.289	1.118	3.27	0.404	0.282	3.56	61.357	−0.309	7.66	22.217	−0.035	9.55	−104
3	−0.099	1.046	1.90	−0.223	0.265	2.05	61.357	−0.309	6.99	33.309	−0.085	6.12	−69
4	−0.050	1.009	1.09	−0.112	0.253	1.15	61.357	−0.309	4.82	43.959	−0.226	4.09	−48
5	−0.014	1.003	0.62	−0.052	0.251	0.65	80.478	−0.823	3.32	56.278	−0.500	2.82	−48
6	−0.002	1.000	0.35	−0.022	0.250	0.36	80.478	−0.823	2.29	52.656	−0.368	1.95	−19
7	0.004	1.000	0.20	−0.014	0.250	0.21	80.478	−0.823	1.58	52.656	−0.368	1.34	3
8	0.009	1.000	0.13	−0.010	0.250	0.13	80.478	−0.823	1.09	52.656	−0.368	0.93	21
9	0.011	1.000	0.11	−0.011	0.250	0.09	80.478	−0.823	0.75	52.656	−0.368	0.64	33
10	0.012	1.000	0.11	−0.012	0.250	0.09	80.478	−0.823	0.52	52.656	−0.368	0.44	35
11	0.013	1.000	0.11	−0.012	0.250	0.09	80.478	−0.823	0.36	52.656	−0.368	0.30	35
12	0.013	0.999	0.11	−0.012	0.250	0.09	—	—	—	—	—	—	35
13	0.013	0.999	0.11	−0.012	0.250	0.09	—	—	—	—	—	—	35
14	—	—	—	0.007	0.250	0.10	—	—	—	—	—	—	−293
15	—	—	—	0.007	0.250	0.10	—	—	—	—	—	—	−293

[a]Notes on Table:

Iteration zero is the initial starting solution derived by independent OLS regressions of each law on the dependent variable.

Iterations 1–10, 12, and 14 are aimed toward refinement of the estimate and attaining convergence.

Iteration 11 results satisfy convergence criterion, rules 3 and 4 eliminated as they explain no observations.

Iteration 13 results satisfy convergence criterion, rule 1 is identified as rule which explains least number of observations and is eliminated on a trial basis.

At iteration 15, rule 1 is tested and shown to contribute significantly. Thus, the final solution is that at iteration 13.

is done by removing the law which explains the least number of observations reapplying Steps (2)−(3), then seeing if the results are statistically different through use of a maximum likelihood ratio test);

c) seeing if any of the laws variances become so small they cannot be estimated.

Step (5). If any laws have been eliminated, go to Step (2), otherwise terminate.

EXAMPLE

The procedure is probably best understood via an example (again motivated by HHB and Bowen 1979). Consider an example in which cars are being assembled. Our simplified car consists of two parts, body and wheels. Assuming that each car takes one body and four wheels, the number of cars (C) that can be manufactured is the minimum of the number of bodies (B) and one-fourth the number of wheels (W). Thus,

$$C = \min \left(\begin{matrix} B \\ 1/4\, W \end{matrix} \right).$$

We may construct an example using this process. Assuming a normally distributed error term for the laws which has mean zero and standard error 0.10; 40 observations were generated for the number of cars manufactured. For expository purposes, a third and fourth "law" were entered, respectively, as the observation number (i.e. 1−40) and a random number. These extra laws, hopefully, will not enter the statistically estimated model, as they have nothing to do with the number of cars manufactured. Table A-1 then gives the results from the application of the law of the minimum procedure to the generated data. The body and wheel functions possess intercepts and slopes which are essentially equal to those from which the data were generated and all unnecessary factors were eliminated. The results indicate the ability of the law of the minimum procedure to identify true relationships, estimate coefficients accurately, and perhaps most importantly, identify and discard spurious explanatory relationships. Similarly, the standard deviations are essentially equal to the figures (0.10) used in data generation.

A Management Analysis of the Pacific Whiting (*Merluccius productus*) Fishery Using an Age-Structured Stochastic Recruitment Model

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This paper applies an age-structured stochastic recruitment model to the Pacific whiting (*Merluccius productus*) fishery off the North American Pacific continental shelf. A policy algorithm has been developed as an aid to management of the fishery which aims to set quotas in such a way as to use strong year-classes in a practical and efficient manner while protecting the stock when it is in a poor condition and environmental conditions do not appear to be conducive to stock improvement in the immediate future. Recruitment in the whiting stock is linked primarily to water temperature in their spawning area. Existing data are used as the basis of a transition matrix for recruitment which depends on both stock level and water surface temperature on the spawning grounds. Comparison with historical data on fishery catch and stock estimates shows model output to be realistic. As a test of the policy algorithm, simulation runs with different quota control criteria in the algorithm were compared with 47-yr runs at constant effort and constant quotas. The policy algorithm was found to protect the stock better and to provide higher average catch per unit effort (CPUE) than the constant effort and quota cases. In the policy algorithm, average yield can be increased at the expense of CPUE. The choice of quota control criteria depends on management preference for improving yields versus having less variable effort and higher average CPUE.

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On applique, dans l'article qui suit, un modèle de recrutement stochastique structuré par âge à la pêcherie de merlu du Pacifique (*Merluccius productus*) au large du plateau continental du Pacifique nord-américain. Un algorithme de politique a été développé pour aider à la gestion de cette pêcherie, qui vise à établir des contingents de façon à utiliser les classes d'âge abondantes d'une manière pratique et efficace, tout en protégeant le stock quand il est en mauvais état et que les conditions du milieu ne laissent pas prévoir d'amélioration dans le futur immédiat. Le recrutement du stock de merlus est avant tout relié à la température de l'eau sur les lieux de ponte. Nous utilisons les données actuelles comme base de matrice de transition pour un recrutement dépendant à la fois du niveau du stock et de la température de surface sur les frayères. Quand on compare les résultats avec les données historiques de capture et d'estimations de stock, on constate que les données de sortie du modèle sont réalistes. Afin de vérifier l'algorithme de politique, des passages machines avec différents critères de

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contrôle des contingents ont été comparés avec des passages de 47 ans à effort et contingents constants. On a trouvé que l'algorithme assurait au stock une meilleure protection et donnait de meilleures prises par unité d'effort (PUE) qu'avec effort et contingents constants. Dans l'algorithme de politique, le rendement moyen peut être augmenté aux dépens des PUE. Le choix des critères de contrôle des contingents dépend des préférences de la gestion devant une amélioration des rendements versus un effort moins variable et des PUE moyennes plus fortes.

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FISHERIES today are managed using a variety of quantitative tools, prominent among which is classical Beverton and Holt yield per recruit analysis. Although this analysis (Beverton and Holt 1957) does consider age-structured populations, its treatment of recruitment as a constant, independent of the stock, is weak. A number of alternative hypotheses based on stock–recruitment theory have been considered, mostly deterministic, including those of Beverton and Holt (1957), Walters (1969), and Ricker (1975). These hypotheses are often not well supported by data (e.g. Cushing 1973). It appears that environmental conditions play an important role in determining year-class strength, and in many instances, stock size appears to play a secondary role (Sissenwine 1977; Van Winkle et al. 1979; Lett and Kohler 1976; Nelson et al. 1976). As variability in year-class strength appears to be an important and regular feature of most commercially important fish stocks, quota and general management policy must begin to consider the resulting year-to-year variability in stock biomass. With this in mind, Getz and Swartzman (1981) developed a population model based on classical Beverton and Holt theory, but in which constant recruitment is replaced by a stock–recruitment transition matrix that reflects the probabilities with which various recruitment levels can arise from different levels of stock abundance. In this model, each element of the age distribution vector is replaced by a probability vector giving the probability that the (biomass) level of that age-class is in one of m arbitrary biomass ranges between zero and some maximum. Instead of computing deterministic yield and stock level, the model computes expected values and variances for each of these variables.

The objectives of the work discussed in this paper are (1) to apply the Getz–Swartzman model to the Pacific whiting (*Merluccius productus*) fishery and specifically to incorporate features of environmental influence of upwelling on recruitment into the model, (2) to evaluate the model by comparison with catch data from 1966 to 1980 and stock estimates from 1973 to 1980, (3) to develop a management policy algorithm which sets quotas in such a way as to use a strong year-class while protecting the stock against the hazard of depletion, and (4) to evaluate the algorithm by comparison with constant effort and constant quota policy alternatives. In this paper, we also discuss some features of the Getz–Swartzman model that have been improved since the initial presentation of the model (Getz and Swartzman 1981). These features allow the model to incorporate many more age-classes than the previous limit of seven. The computer run time of the model has been considerably reduced, thus making the policy algorithm feasible. Also, certain anomalies, resulting from the discretization of the stock–recruitment relationship, have been eliminated.

Management problems associated with the Pacific whiting offshore stock and fishery appear to lend themselves well to an application of a slightly modified version of the Getz–Swartzman model as this stock exhibits high variability in year-class strength and its recruitment appears to be loosely linked to stock level.

A detailed description of the life history of and fishery for Pacific whiting is given by Bailey et al. (1982). Briefly, the coastal stock of Pacific whiting occupies the continental shelf and slope area of the California current system, ranging from a feeding area off Vancouver Island in the north to a spawning area as far south as the southern tip of Baja California (Fig. 1). In autumn, adult whiting make an annual migration from the summertime feeding grounds off the Pacific northwest coast to winter spawning grounds off the coasts of southern California and Baja California. In spring and summer, large adult fish migrate northwards as far as central Vancouver Island and juveniles remain off central and northern California. Oceanographic conditions at the time of spawning appear to play a major role in the recruitment to the exploitable stock of Pacific whiting. Year-class strength is highly variable. Between 1973 and 1980, estimated recruitment at age 3 varied from a low of 0.3 billion to a high of 1.7 billion individuals.

Before 1966 the whiting stock was largely unexploited. Since then, Pacific whiting has been the target of a large foreign fishery off the west coast of the U.S. and Canada. This fishery, which runs from April to October, is managed in the United States under a Fishery Management Plan for groundfish (Pacific Fisheries Management Council 1982). Estimated catches have ranged from 91 to 236 thousand metric tons (t) (Bailey et al. 1982). The average annual all-nation reported catch for 1966–80 was 162 thousand metric tons.

Model Description and Modifications

The model developed by Getz and Swartzman (1981) can be briefly summarized as follows. Notation is presented with the text and is summarized in a glossary in Appendix A.

a) The number of individuals in each of n age-classes at time k is characterized by a probability vector $\mathbf{P}_i(k)$, $i = 1, \ldots, n$, whose jth element $P_{ij}(k)$, $j = 1, \ldots, m$, represents the probability that the actual size of this age-class is in the interval

$$[((j-1)/m)\,\hat{x}_i(k),\ (j/m)\,\hat{x}_i(k)].$$

The maximum population level $\hat{x}_i(k)$ for each age-class i is calculated by accruing natural and fishing mortality via a

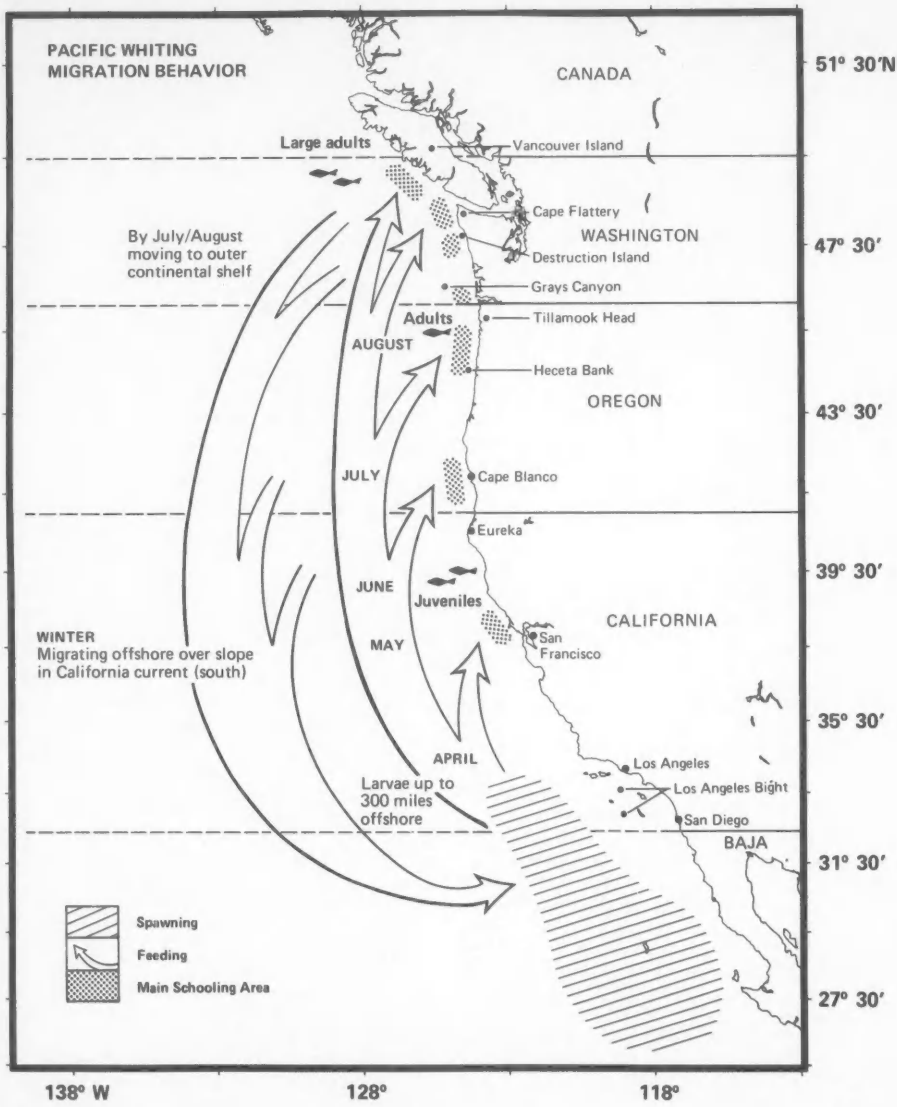

FIG. 1. Migratory patterns of Pacific whiting (*Merluccius productus*).

Beverton and Holt type analysis, i.e.

$$(1)\quad \hat{x}_{i+1}(k+1) = e^{-[\alpha_i + q_i \nu(k) \tilde{t}]}\, \hat{x}_i(k) \qquad i = 1, \ldots, n-1.$$

where α_i, q_i, $\nu(k)$, and $\tilde{t}$ are, respectively, the natural mortality rate, catchability coefficient, fishing effort, and length of fishing season as a fraction of the total season. The maximum recruitment $\hat{x}_1$ is a constant over time ($k = 0, 1, 2, \ldots$) and is determined from recruitment data. The probability vector $\mathbf{P}_i(k)$ is carried forward as the age-group passes into the next year-class, i.e.

$$(2)\quad \mathbf{P}_{i+1}(k+1) = \mathbf{P}_i(k) \qquad i = 1, \ldots, n-2.$$

with the only exception being $\mathbf{P}_n(k+1)$ for the case when the nth age-class consists of individuals not only of age $n-1$ but

TABLE 1. Parameter values used in the simulation runs.

	Parameters	Value for Pacific whiting
n	No. of age-classes	8 (ages 3, 4, . . . , 9, 10−12)
r	No. of years that recruitment is delayed after spawning	3
m	No. of age-class subdivisions	6
m_s	No. of parent stock subdivisions	8
$\hat{x}_1$	Maximum no. of recruits	2.4×10^9
$\hat{S}$	Maximum fecund stock biomass (kg)	1.5×10^9
$\bar{t}$	Length of fishing season (yr)	0.42

	Ages							
Parameters	3	4	5	6	7	8	9	10−12
Natural mortality rates α_i (yr^{-1})	0.278	0.210	0.195	0.257	0.357	0.457	0.557	0.657
Catchability coefficient q_i (1000 vessel days effort)$^{-1}$	0.0107	0.0283	0.0338	0.0731	0.1021	0.1695	0.1836	0.1667
Maturity coefficient c_i (fraction of sexually mature individuals in each age-class)	0.50	0.75	1.00	1.00	1.00	1.00	1.00	1.00
Weight coefficients w_i (g)	483	613	717	800	854	906	932	955

older [see Getz and Swartzman (1981) for details].

b) The fecund stock biomass level in the fishery at time k is characterized by a probability vector $\mathbf{P}_s(k)$ whose jth element $p_{sj}(k)$, $j = 1, \ldots, m_s$, represents the probability that the actual fecund stock biomass level is in the jth range

$$\left[\left(\frac{j-1}{m_s}\right)\hat{S}, \left(\frac{j}{m_s}\right)\hat{S}\right]$$

where $\hat{S}$ is the maximum fecund stock biomass level. The value of S is calculated using the expression

$$(3) \quad \hat{S} = \sum_{i=1}^{n} c_i w_i \hat{x}_i$$

where c_i is the fraction of sexually mature fish and w_i is the average weight per individual in the ith age-class, whereas the $\hat{x}_i$ are obtained from (1) for the case $v = 0$ (i.e. no fishing mortality), with the value of $\hat{x}_1$ being the maximum recruitment observed in the fishery.

c) The probability vector $\mathbf{P}_1(k+1)$ [not obtainable from (2)], characterizing the probability distribution of the new recruits at time k, is obtained from the spawning stock using a stock−recruitment probability transition matrix approach. The elements t_{ij}, $i = 1, \ldots, m$; $j = 1, \ldots, m_s$, of this transition matrix $\mathbf{T}$, represent the probability with which a fecund stock in the jth biomass range will result in the number of recruits falling into the range

$$\left[\frac{l-1}{m}\hat{x}_1, \frac{l}{m}\hat{x}_1\right].$$

Thus, in general, if newly spawned individuals are only recruited to the fishery at age r, then it follows that

$$(4) \quad \mathbf{P}_1(k+1) = \mathbf{T}\mathbf{P}_s(k+1-r).$$

d) In the model the fishing season (April−October) occurs first with both fishing and natural mortality accruing and expected yield and yield variance being computed. The spawning season (January−March) thus occurs at the end of a time step with the stock probability density function being computed at the end of the year for purposes of computing the recruitment probability density function. Updating occurs after spawning to supply the new age-class distribution for the coming fishing season.

e) The major computational problem posed by this model is the calculation of $\mathbf{P}_s$ from $\mathbf{P}_i$, $i = 1, \ldots, n$. This actually is the discrete analog of a convolution of the sum of the age-class random variables x_i multiplied by $c_i w_i$ to produce the stock random variable. A method for computing $\mathbf{P}_s$ from $\mathbf{P}_i$, based on the assumption that the vectors $\mathbf{P}_i(k)$ are independent across i (this assumption improves as the correlation between stock and recruitment levels is reduced) is discussed in Getz and Swartzman (1981). The time required to complete this computation is a linear function of m^n, which essentially restricts the size of problems to those in which $n \leq 6$

TABLE 2. Stock–recruitment probability transition matrices. The transition matrix elements t_{ij} represent the probability that a spawning stock biomass in subdivision j (≤8) will result in the number of recruits being in subdivision l (≤6).

Average no. recruited (billions)	Recruitment level								
		Cold + intermediate							
2.2	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.8	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.4	4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.0	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.6	2	0.00	0.45	0.60	0.65	0.68	0.68	0.68	0.68
0.2	1	1.00	0.55	0.40	0.35	0.32	0.32	0.32	0.32
Spawning stock levels		1	2	3	4	5	6	7	8
Avg biomass (mt)		0.09	0.28	0.47	0.66	0.84	1.03	1.22	1.41
		Warm							
2.2	6	0.00	0.00	0.00	0.05	0.10	0.10	0.10	0.10
1.8	5	0.00	0.00	0.05	0.07	0.15	0.15	0.15	0.15
1.4	4	0.00	0.00	0.15	0.15	0.15	0.15	0.15	0.15
1.0	3	0.00	0.20	0.20	0.23	0.20	0.20	0.20	0.20
0.6	2	0.14	0.60	0.45	0.35	0.25	0.25	0.25	0.25
0.2	1	0.86	0.20	0.15	0.15	0.15	0.15	0.15	0.15
Spawning stock levels		1	2	3	4	5	6	7	8
Avg biomass (mt)		0.09	0.28	0.47	0.66	0.84	1.03	1.22	1.41

[i.e. populations with six or fewer fishable age-classes for reasonable values of m (e.g. $m = 6$)]. A modification of this approach based on a "pairs algorithm" has reduced computational time to a linear function of $m^2\,2^{2(K'-1)}$, where K' is the integer satisfying $2^{K'-1} < n \leq 2^{K'}$. The mechanics of this algorithm are described in Appendix B. With only a small sacrifice in accuracy, it allows us to deal with problems involving up to 32 age-classes ($n \leq 32$).

f) Another improvement to the model is the use of linear interpolations to smooth anomalies which arise from discretizing age-class and stock-biomass levels (see Appendix B). These have been used in estimating expected stock and yield levels, and associated variances as described in Getz and Swartzman (1981) where, for example, expected yield Y is obtained in terms of effort v via the formula

$$E[Y(k+1)] = v(k) \sum_{i=1}^{n} w_i q_i (1 - e^{-[\alpha_i + q_i v(k)]\bar{t}}) \hat{x}_i(k) \cdot \sum_{j=1}^{m} \left[\frac{j - 0.5}{m}\right] p_{ij}(k) / [\alpha_i + q_i v(k)]. \quad (5)$$

Our program also incorporates a 'catch quota option' which allows us to estimate $v(k)$ once an a priori value for $E[Y(k+1)]$ has been selected.

The relationship between yield and effort is given in equation (5) and shows that it is not possible to solve explicitly for the effort that gives a desired yield. An algorithm was devised which finds the effort level corresponding to a given yield quota. The algorithm must consider whether the yield–effort curve is increasing or decreasing with increasing effort and whether it is above or below the desired yield. The algorithm was set to change effort by a constant increment or decrement. The final effort chosen was the smallest one that produced a yield less than or equal to (and as close as possible to) the yield quota.

Application to the Whiting Fishery

The Getz–Swartzman model, modified as discussed above, was applied to the northwest U.S. coast whiting fishery. Model parameters are given in Table 1. Specific age-dependent parameters (α_i, q_i, w_i; $i = 1, \ldots, 8$) were derived from the Option 2 (modified weight–age, Laevastu–Cushing natural mortality) cohort analysis reported by Francis (1982). Because this cohort analysis was performed on nine age-classes (ages 3–11), we felt that it was important to retain this structure in the management analysis (although we combined ages 10 through 12). The maximum number of recruits and maximum parent (fecund) stock biomass (S) were set to reflect levels that would be expected to occur under optimal production conditions and without the fishery operating. These levels are well above the maximum values estimated during the period (1973–80) from which parameter estimates were made. The age-specific catchability coefficients (q_i; $i = 1, \ldots, 8$) were modified from the annual estimates, produced in the cohort analysis, so that they could be applied to the 6-mo fishing season used in the management analysis, whereas fishing effort is given in units of 1000 vessel-days (kd) on the fishing grounds. The maturity coefficients were estimated by K. Bailey (School of Fisheries, WH-10, University of Washington, Seattle, WA 98195). There are eight age-classes in this model which correspond to ages 3, ..., 9, 10–12. Thus $i = 1$ corresponds to age 3 whiting and $i = 8$ corresponds to age 10–12 whiting.

The estimates of the elements of the stock–recruitment probability transition matrices are listed in Table 2 and are

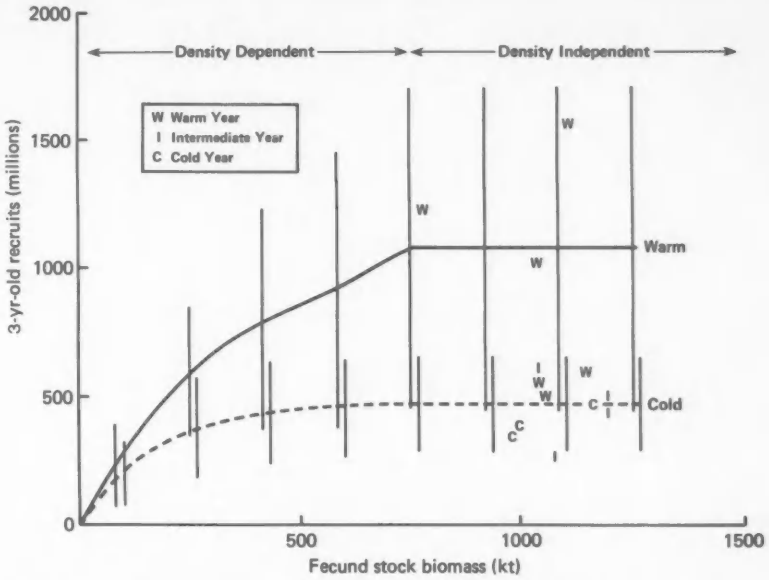

FIG. 2. Stock–recruit relationships of Pacific whiting used in the model (mean ± 1 SD). Stock–recruit data for 1966–77 are also shown for comparison.

based on data depicted in Fig. 2. There are two matrices, one for "cold" and one for "warm" years to be discussed below. These matrices are based on the hypothesis, supported by current data, that "cold" water temperatures on the spawning grounds result in relatively lower average recruitment with less variability than in years of "warm" water temperatures.

Bailey (1981) demonstrated that whiting recruitment is inversely correlated to the level of wind-driven Ekman transport on the spawning grounds at the time of spawning. We have reasoned that offshore transport is positively correlated with the level of upwelling which, in turn, is negatively correlated with sea surface temperature, as colder bottom water will be brought to the surface during upwelling. Therefore, years of "cold" water temperatures on the spawning grounds are assumed to be years of high offshore transport and low larval survival, and years of "warm" water temperatures are assumed to be years of low offshore transport and higher although more variable larval survival. The average sea surface temperature from January to March in the Los Angeles Bight is used as our reference temperature.

Temperature data were available from 1931 to 1979 and a frequency histogram of temperatures was trimodal. On this basis, the data were divided into cold (13.4–14.7°C), intermediate (14.7–15.6°C), and warm (15.6–16.9°C) classes so that each interval roughly contained one of the three modes found in the histogram.

A plot in Fig. 2 of fecund stock biomass (s) against recruitment at age 3 coded by the three temperature intervals (warm, intermediate, cold) provides qualitative evidence in support of the hypothesis proposed at the beginning of this section. Recruitment from cold and intermediate years appears low and relatively invariable, whereas for warm years it is higher and more variable. In neither case is there any indication of a stock effect on recruitment. Two separate stock–recruit probability transition matrices were estimated from the data in Fig. 2, one for cold plus intermediate years and one for warm years.

To estimate the elements, t_{ij}, of the stock–recruitment probability transition matrices (Table 2), relationships between values of stock biomass, surface water temperature at the time of spawning, and subsequent recruitment to the fishery 3 yr later were developed. The probabilities in Table 2 were estimated by placing an $m \times m_s$ grid over the data in Fig. 2. The probabilities are then the frequencies of points in each column of the grid. As seen from Fig. 2, there are not sufficient data for either the warm or cold years to obtain accurate estimates for the t_{ij}'s. Therefore, the t_{ij}'s are estimated such as to give the same expected value and variance as the data in Fig. 2.

To obtain as many stock–recruit data points as possible, relative and absolute measures of both stock biomass and subsequent recruitment were used. The relative measures were adjusted according to regressions obtained for years when both measures were available. The relative measures were from Bailey et al. (1982), whereas absolute measures were obtained from Francis (1982). The relative stock measure was larval abundance produced by that stock on the spawning grounds (CALCOFI and Soviet cruises) during January after being adjusted for post-January spawning. The relative recruit measure is an index of year-class strength obtained from the age distribution of several years' catch surveys.

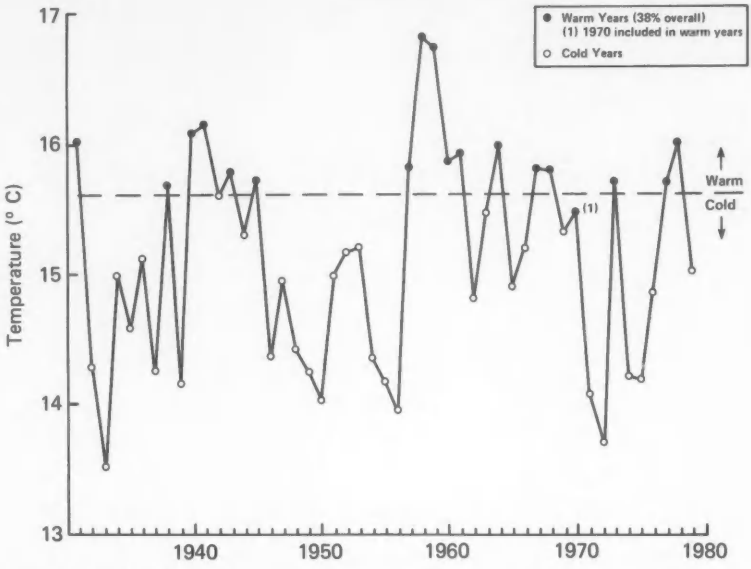

FIG. 3. The 1931–79 mean January–March sea surface temperature (°C) in Los Angeles Bight.

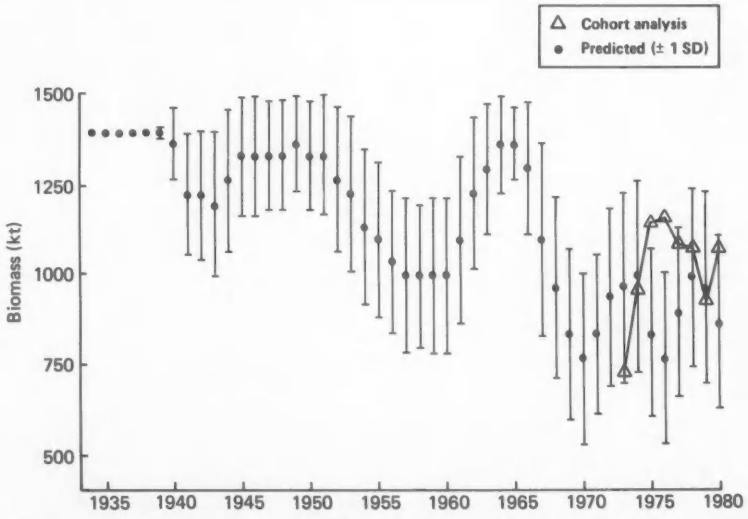

FIG. 4. Expected fecund stock biomass of Pacific whiting (±1 SD). Fecund stock estimates from cohort analysis (Francis 1982) for 1973–80 are also shown for comparison.

For the runs reported in this paper, estimates of the elements of the probability transition matrices were made based on fecund stock level data in the range of 0.7–1.2 mt. Over this stock range, recruitment was assumed to be independent of stock and only dependent on temperature at the time of spawning (see Fig. 2). In the stock range of 0–0.7 mt (values below fecund stock levels actually observed), it was assumed that the expected value of the probability density function generated by the estimates of t_{ij}, the elements of the transition matrix, would roughly follow negative exponential stock–recruit curves of the form shown in Fig. 2. This assumption was made following the suggestion of Shepherd (1982). The

probabilities for the lower stock range were then chosen to meet this criterion for expected recruitment and maintain comparable levels of variation (i.e. same coefficient of variation). The resultant stock−recruitment probability transition matrices for cold plus intermediate and warm years are given in Table 2.

As no data were available for low stock levels (i.e. $s < 0.7$ mt), two other options (besides the negative exponential model) were used for the t_{ij}'s in this range. In the first case, recruitment was assumed independent of spawning stock and in the second the decline in recruitment was assumed linear. The first of these options was felt to be unduly optimistic and the second somewhat pessimistic. The negative exponential option was an intermediate relationship. In absence of data over the 0−0.7 mt fecund stock biomass range, it is difficult to determine the most likely behavior of the fish stock under heavy fishing pressure. The Getz−Swartzman model is sensitive to the transition matrix probabilities in the low stock range and the idea of probing the fishery by way of management experiments (Walters 1981) to force the stock into a low range is one that has some relevance but is not considered here.

Historical runs of the model were made over a 47-yr period (1933−80) for which sea surface temperature data at the time of spawning were available. Driving variables for the population and yield model were (a) effort levels in thousands of standard vessel days from 1966 to 1980, the years of the fishery (Bailey et al. 1982), and (b) classification of environmental conditions on the whiting spawning ground into warm or cold for 1931 to 1977 based on mean January−March surface temperatures in the LA Bight (Doug McClain, National Marine Fisheries Service, Southwest Fisheries Center, Pacific Environmental Group, P.O. Box 831, Monterey, CA 93942). Figure 3 is a plot of the 47-yr time series of temperature at the time of spawning; Fig. 4 is a plot of the means and standard deviations of the simulated fecund stock biomass for 1934−80; and Fig. 5 is a plot of the means and standard deviations of simulated catches along with the observed catches for the history of the fishery (1966−80). One thing that is important to note is that whereas the frequency of warm years was 38% between 1931 and 1979, it was 48% between 1956 and 1979, the time span within which the year-classes produced could have affected the productivity of the fishery. As will be seen later, this is very important for the estimation of long-term stock production.

It is interesting to observe the fluctuations in stock biomass predicted by the model (Fig. 4). The period between peaks and troughs is around 20 yr, a reflection of the apparently periodic fluctuations in environmental conditions on the spawning grounds (Francis et al. 1982). The initial conditions for the run (1933−38) were set arbitrarily to large stock levels to represent a virgin stock. The model, therefore, more accurately represents variations in the stock beginning around 1940 or 1941 after the effects of initial conditions have been damped out.

Expected fishery yields from the model agree quite well (always within or close to within 1 SD) with the observed yields for 1970−80, whereas for 1966−69 the yields calculated by the model are consistently larger than those reported for the fishery. This inconsistency in the early years of the fishery could be due to one or more of the following factors:

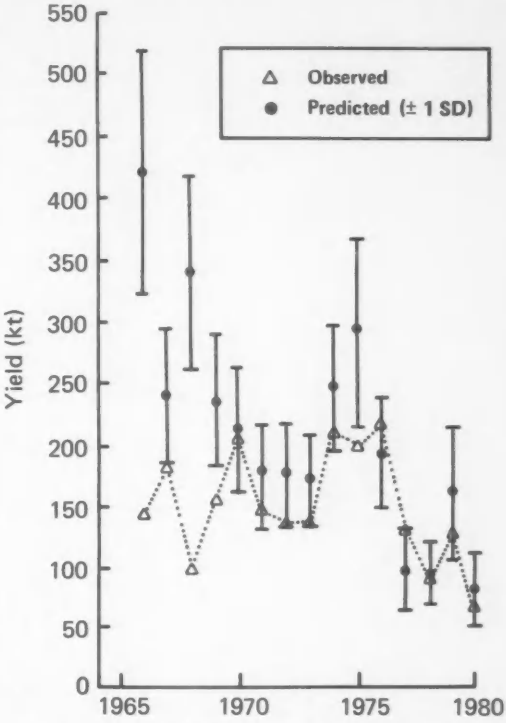

FIG. 5. Expected Pacific whiting yield (± 1 SD) from historic simulation for 1965−80 compared with reported catches (kt).

1) The gear used by the Soviet fishery changed from predominately side trawlers at the outset to exclusively factory stern trawlers after 1972. A rough attempt was made to standardize effort (Bailey et al. 1982) but the fishing power factors may be inaccurate.

2) Effort may have been quite inefficient in the early years of the fishery due to a lack of experience in locating good fishing grounds and deploying the gear to catch the fish.

3) There may have been an underreporting of the catch in the early years.

4) The model may have overestimated the status of the fishable stock at the time of the initiation of the fishery. Note that the simulated stock is especially high at the time (1966) the fishery started.

It should be stressed that parameters were estimated based on data collected over the last 20 yr. Thus, the trend in stock biomass in Fig. 4 reflects what might have been expected to occur over a 47-yr period given parameters based on stock conditions over only the past 20 yr.

Equilibrium Analysis

The concept of maximum sustainable yield (MSY) has

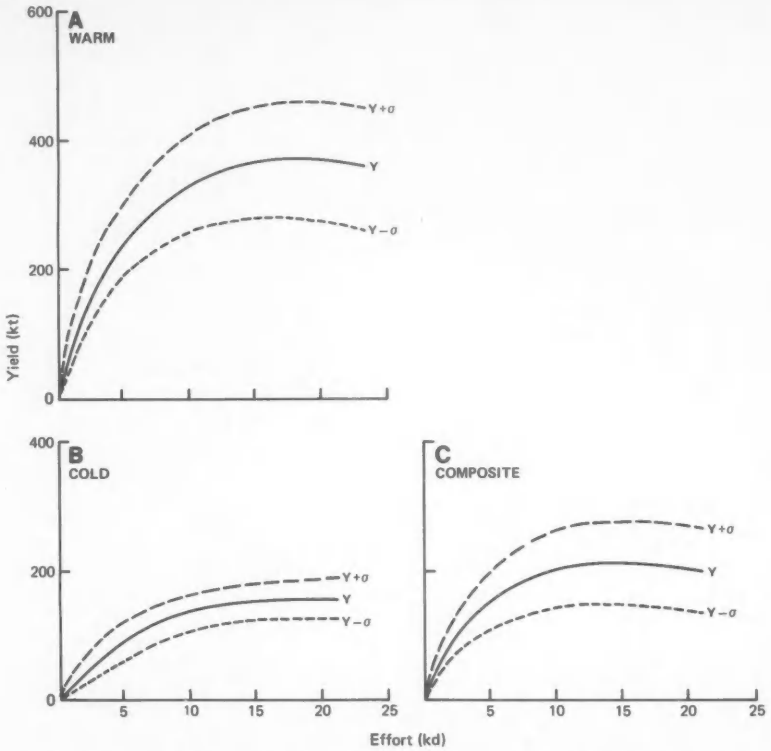

FIG. 6. Expected sustainable yield of Pacific whiting (±1 SD) as a function of effort for warm, cold, and composite years.

served as an important reference point or target for fisheries managers (NPFMC Fishery Management Plans 1979, 1980) and also is an important feature of stock–recruit and other fishery management models (Clark 1976; Ricker 1975). By running the model at various constant efforts until equilibrium is reached, equilibrium yield/effort curves can be produced and the maximum expected sustainable yield can be calculated. This was done for three fisheries in Getz and Swartzman (1981) and the MSY value compared favorably with MSY obtained from a deterministic analysis for one of these fisheries (Getz 1980).

Analyses were conducted for the Pacific whiting fishery for warm, cold, and average temperature conditions. The average transition matrix was taken as a composite matrix of warm and cold year matrices weighted by the probability of warm (0.38) and cold (0.62) temperatures. Expected yield, yield variance, total stock, fecund stock, and desirable stock (all adults over age 5), and their variances were computed for each effort level. The desirable stock level at expected MSY was used as a target level for a management policy algorithm as discussed below.

With the above analysis, we were able to investigate what the equilibrium yield–effort relationship might look like under a long run of cold years (the worst foreseeable conditions), a long run of warm years (the best foreseeable conditions), and a long run of "average" years. The results are given in Fig. 6 for all three sets of conditions. The curves displaying mean yield as a function of effort are bracketed by curves representing one standard deviation on either side of the mean. The results indicate the large variability in productivity of the stock as a function of the environmental conditions. Over the last 40–50 yr, the longest run of consecutive cold years was 11 (1935–46) and the longest run of consecutive warm years was 5 (1956–61). The MSY level for cold years provides insight into the loss of productivity during a run of cold years such as the period 1935–46, and this provides an appropriate base stock level for protecting the fishery (i.e. the probability the fished stock falls below this level should be small), as is discussed more fully in the next section.

A Management Algorithm

In this section, a management policy algorithm for setting catch quotas for Pacific whiting is developed, implemented using our model, and compared with the simulated behavior

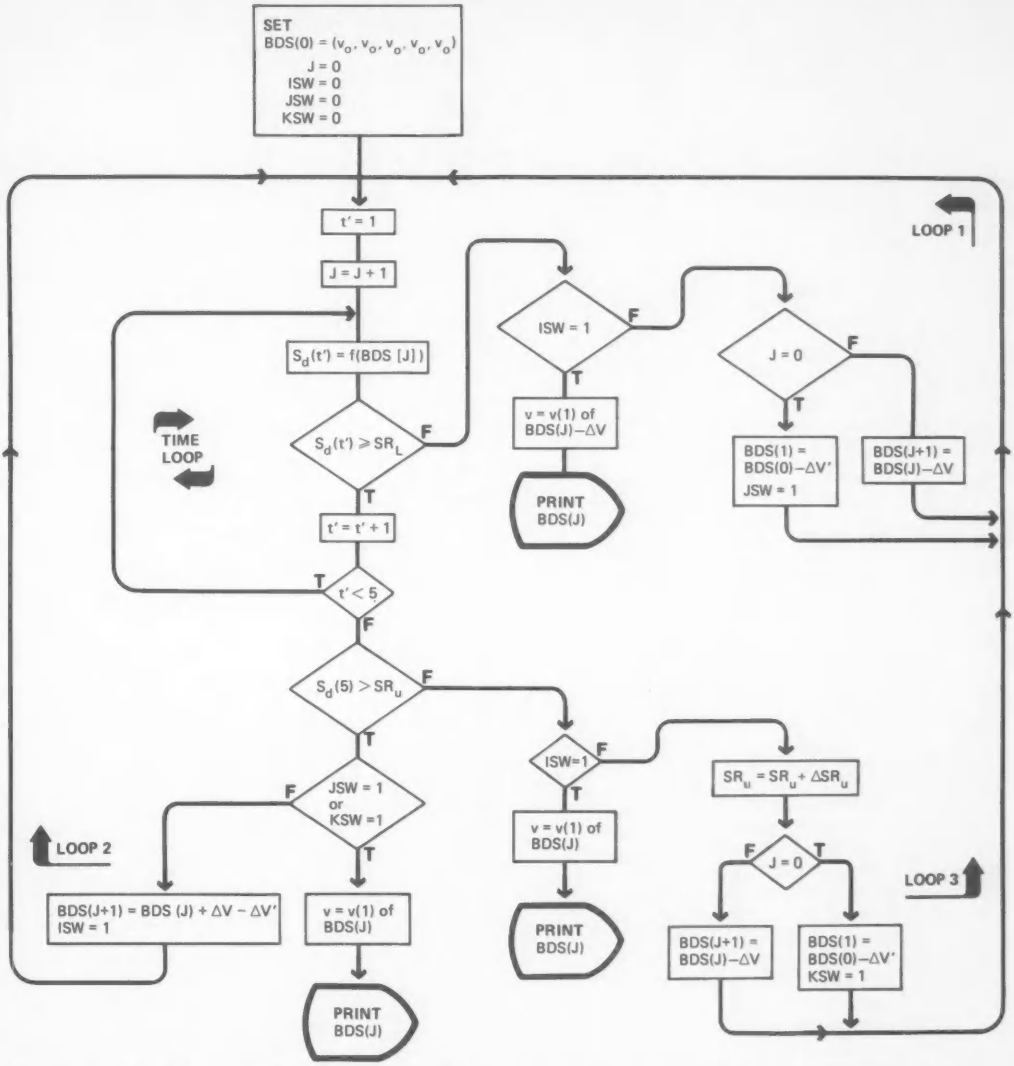

FIG. 7. Flow chart of the Pacific whiting management policy algorithm. Notation is in Appendix B. The loops denote the three cases which are below SR_L (Loop 1), above SR_u (Loop 2), and between SR_L and SR_u (Loop 3).

of the stock and fishery under constant yield quota and constant effort quota management options. The aim of the new management policy is to

1) fully exploit strong year-classes in the fishery, and

2) protect the stock when it is in poor condition and environmental conditions do not appear conducive to stock improvement in the immediate future by spreading the reduced yields over several years.

We use a 5-yr look-ahead algorithm that projects the stock 5 yr ahead from its present level. This period of time was chosen because it is the time the cohort spawned in the present year takes to be fully recruited into both the fishery and the fecund stock. The projection uses information on temperatures over the previous 3 yr to forecast recruitment for the first 3 yr of the algorithm. The 4th year is forecast using the present year's temperature and the conditional probability that

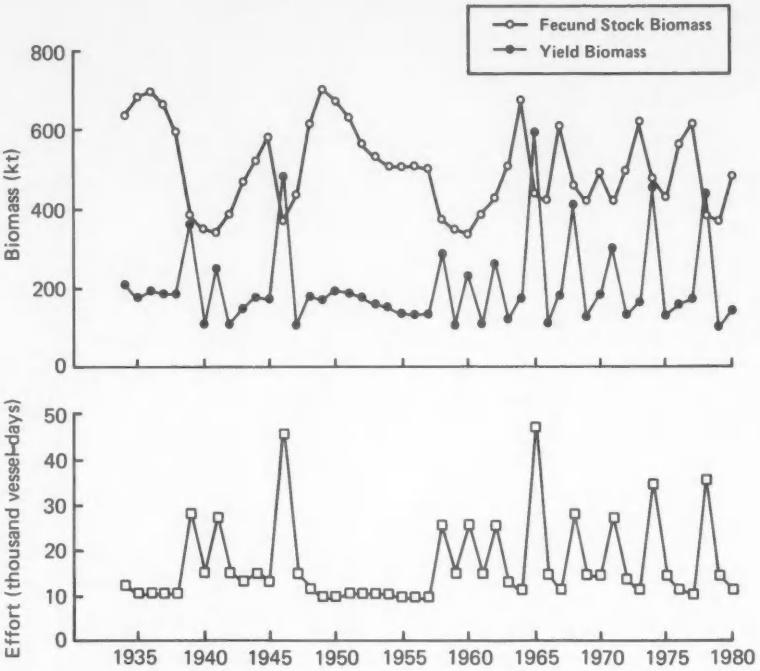

FIG. 8. Expected fecund stock, yield biomass, and fishing effort over the period 1934–80 for the policy algorithm with $SR_u/SR_L = 293/155$.

next year will be "warm" or "cold." This is based on the observation that warm and cold years tend to come in runs from which Markovian probabilities for warm and cold years following each other can be estimated (see Fig. 3). For the 5th year of the algorithm, recruitment is projected using the average year (composite) probability transition matrix.

The algorithm operates in the following way:

1) Define a desirable stock as that portion of the total stock (based on marketing and/or processing criteria) which one wishes to monitor as an indicator of stock condition.

2) Set a catch quota for next year as high as possible under the conditions that:

a) the probability that the desirable stock drops below a critical lower threshhold, SR_L, over the next 5 yr is less than a predetermined level and

b) the expected desirable stock is as close as possible to a desirable stock level, SR_u, at the end of 5 yr, without violating condition (a).

Lower and upper stopping rules are defined in the algorithm based on these threshholds to indicate when an acceptable yield has been reached.

In our case the lower stopping rule, SR_L, was chosen initially to be the desirable stock level at expected MSY under the cold weather probability transition matrix (155 kt), whereas the upper stopping rule was the stock level at expected MSY under the average year probability transition matrix (293 kt). In later runs, other stopping rules were used for reasons explained below.

It is known that in certain fisheries pulse fishing produces greater biomass yield than sustained yield policies (Clark 1976). Our algorithm is designed to be equivalent to pulse fishing when the stock is at high levels. When the stock is weak, however, instead of allowing fast stock recovery with very low yield quotas, we spread the recovery over several fishing seasons, allowing intermediate yield levels the coming year. Thus, the policy algorithm does not maximize biomass yield during periods of low stock levels; rather it tries to ensure that the fishery can remain operative during these times.

The algorithm is presented as a flow chart in Fig. 7. Basically, three cases occur, and are labeled loop 1, loop 2, and loop 3 in Fig. 6. In loop 1, the stock drops below the lower stopping rule in any of the next 5 projected years. Effort is then reduced in each year until the stock is both above the lower stopping rule in every year and above the upper stopping rule after 5 yr. In loop 2, the stock level is originally above the upper stopping rule after a 5-yr projection. Effort in the 1st year of the 5-yr projection is increased until further effort increase would drop the expected stock below the upper stopping rule. In loop 3, the stock after a 5-yr population projection is below the upper stopping rule (but above the lower stopping rule for all 5 yr). In this case, effort is reduced

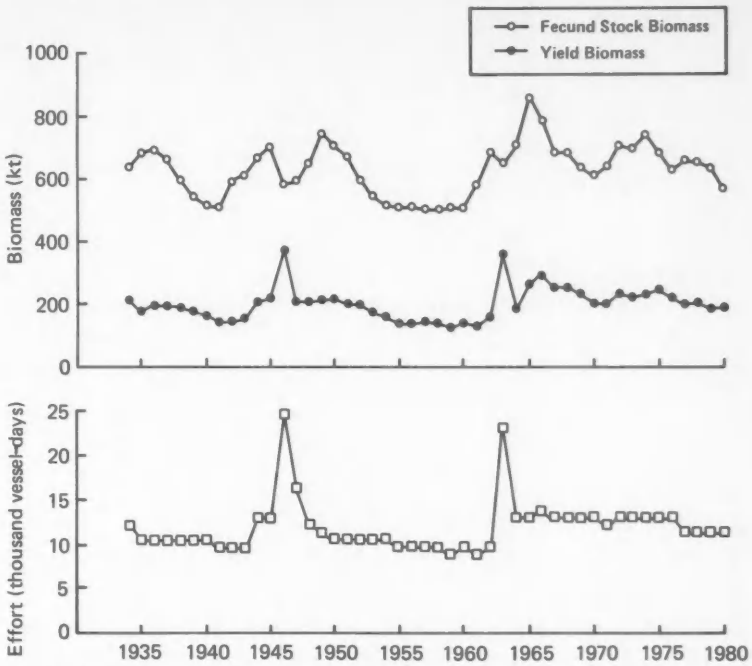

FIG. 9. Expected fecund stock, yield biomass, and fishing effort over the period 1934–80 for the policy algorithm with $SR_u/SR_L = 293/293$.

and the upper stopping rule SR_u is also reduced in decrements of ΔSR_u until the stock level just exceeds the adjusted upper stopping rule. In all three cases the algorithm sets effort for the current year as the largest 1st year's effort in the 5-yr projection that after 5 yr produces an expected stock just above the upper stopping rule.

In Fig. 7 the base decision sequence BDS(J) denotes a 5-element vector giving the effort for each of the 5 yr of the future projection for the Jth iteration of the algorithm. The initial condition is BDS(0) = (v_o, v_o, v_o, v_o, v_o) where v_o is chosen to be the effort level for expected MSY for average years taken from the equilibrium analysis. Changes in the base decision sequence as part of the algorithm are denoted using two 5-element vectors $\mathbf{V} = (\Delta v, \Delta v, \Delta v, \Delta v, \Delta v)$ and $\Delta\mathbf{V}' = (0, \Delta v, \Delta v, \Delta v, \Delta v)$ where Δv is a parameter for the increment or decrement of effort in the policy algorithm. Increases in the 1st year are accomplished by incrementing the BDS by $\Delta\mathbf{V} - \Delta\mathbf{V}'$ (see Fig. 7).

In our implementation, we set $v_o = 35$ and $\Delta v = 2$. For the reduction of the upper stopping rule in steps of ΔSR_u, we chose $\Delta SR_u = \frac{SR_u - SR_L}{60}$, thus allowing a maximum of 60 iterations of the policy algorithm for each year.

Results and Evaluation of Policy Algorithm

To compare the performance of the management algorithm with constant catch or effort quota policies, runs were made over a 47-yr time period from 1934 to 1980. Initial conditions were those estimated to occur at maximum equilibrium yield under the average year probability transition matrix. Recruitment from 1934 through 1980 was affected by observed environmental conditions on the spawning grounds from 1931 through 1977 as in the historical runs.

For all runs of the management algorithm, the desirable stock was the biomass of individuals of 5 yr and older. This decision was made because both full recruitment to the fishery and full maturity in the population are estimated to occur at age 5 (Bailey et al. 1982). We, therefore, decided that the critical biomass for a healthy stock should depend on the number of fish 5 yr and older. Also, harvesting fish 5 yr and older is economically preferable to harvesting younger fish. Initially two management algorithm runs were made. The first was with the upper stopping rule set at the desirable stock biomass that produced maximum expected equilibrium yield under the average year probability transition matrix (SR_u = 293 kt) and the lower stopping rule set at the desirable stock level which maximized the expected equilibrium yield under the cold year probability transition matrix (SR_L = 155 kt). The second management run had $SR_u = SR_L$ = 293 kt. These runs are denoted by SR_u/SR_L, i.e. 293/155 and 293/293.

Results are presented in Fig. 8–10 and Table 3 for the two management algorithm runs and an analogous constant yield

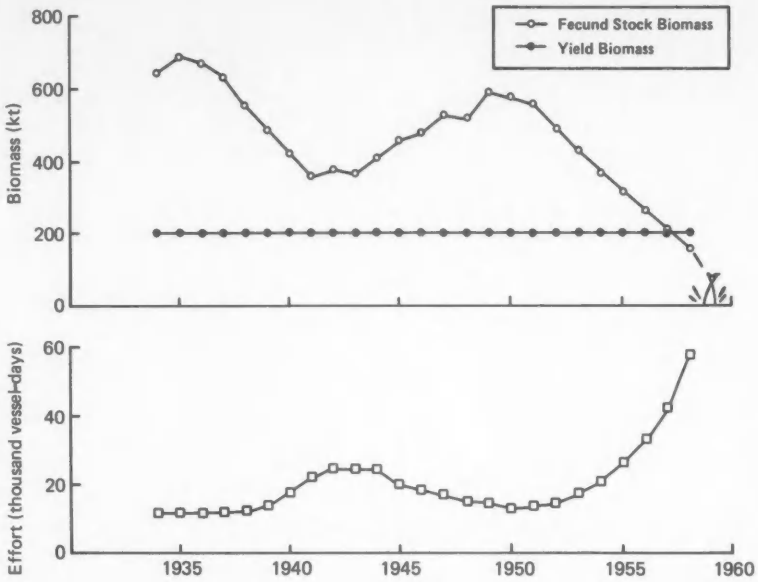

FIG. 10. Expected fecund stock, yield biomass, and fishing effort over the period 1934–59 for a constant annual yield quota of 200 kt.

quota run. The 293/155 (Fig. 8) and 293/293 (Fig. 9) management runs produced average yields of 206 kt and 200 kt, respectively. The corresponding constant yield quota run of 200 kt (Fig. 10) decimates the stock around 1959 during a long run of consecutive cold years. Although a reduction in the constant yield quota to 175 kt did not decimate the stock, the stock was at times seriously reduced from MSY levels. The following points emerge from an analysis of the simulation results:

1) The 293/293 run yields the most desirable results of the three simulations over the long term as it:

a) has a significantly higher average CPUE (Table 3);

b) produces a more stable fishery and desirable stock (a stability that one should be willing to trade for a slightly higher expected yield resulting when the lower stopping rule is decreased (293/155 — Fig. 8); and

c) maintains the desirable (and fecund) stock at a much safer level [$E(s)$, the expected fecund stock biomass, never drops below around 500 kt in Fig. 9] than any of the other runs [$E(s) < 500$ kt for 51% of the simulated years in run 293/155 — see Fig. 8].

2) A policy of constant catch quotas (Fig. 10) is wasteful of the surplus stock biomass during runs of favorable environmental conditions and dangerous to stock survival during runs of unfavorable environmental conditions.

3) To take advantage of favorable stock conditions under this algorithm requires that the fishery be able to switch to a high level of effort within a relatively short period of time (several months). Similarly, to protect the stock (and subsequent fishery) in times of unfavorable stock conditions, the fishery must be able to operate at reduced effort levels over several seasons. However, current knowledge of the magnitude of prerecruit age-classes, as well as the prediction of temperature conditions on the spawning ground for the following year, help to provide lead time for both fishery managers and operators to adjust expected quota levels over a 5-yr time horizon.

A 47-yr run was made with effort fixed at a constant value of 14.7 thousand vessel-days per year, the equilibrium effort level estimated to produce MSY under average environmental conditions. Results are compared in Table 3 ("const effort" column) with the runs shown in Fig. 8–10. The resultant average yield of 203 kt was very slightly higher than the 293/293 policy run. However, the constant effort policy produced a definite reduction in efficiency of exploitation, as evidenced by the lower CPUE when compared with the 293/293 management algorithm (see Table 3).

Finally, to make a direct comparison of the management algorithm with a long-term constant yield quota run which does not decimate the stock, a run was made with equal upper and lower stopping rules chosen to produce an average 47-yr yield of around 175 kt. This turned out to be $SR_L/SR_u = 400/400$, the results of which are also given in Table 3. Comparing this run with a simulated constant annual quota of 175 kt shows (Table 3) that the 400/400 algorithm produces a higher and less variable CPUE.

Conclusions

The foregoing analysis demonstrates that the Getz–

TABLE 3. Comparison of yield, effort, and CPUE between policy algorithm, constant effort, and constant quota runs.

		293/293	293/155	400/400	Const. effort	Const. quota	Const. quota
Yield (kt)	Mean	200	206	178	203	200[a]	175
	SD	53	109	50	33	—	—
	CV	0.27	0.53	0.28	0.16	—	—
Effort (1000 vessel days)	Mean	11.9	16.8	7.6	14.7	>20[a]	10.2
	SD	3.0	9.4	1.8	—	—	4.4
	CV	0.25	0.56	0.24	—	—	0.43
CPUE (mt/vessel day)	Mean	16.8	12.9	23.2	13.8	<10[a]	17.2
	SD	2.0	3.6	2.5	2.2	—	6.7
	CV	0.12	0.28	0.11	0.16	—	0.34

[a]Stock crashed in 1959.

Swartzman model, embedded in the management algorithm depicted in Fig. 7, provides a significant aid in the analysis and management of a fishery, such as Pacific whiting, that exhibits considerable environment-dependent recruitment variability. This represents an extension of the model from previous applications (Getz and Swartzman 1981) where only stock was considered for recruitment. Model behavior compared favorably with yield data from 1966 to 1980. In addition, the management policy algorithm presented in the previous section provides a more rational approach than constant yield quota management as it takes advantage of strong year-classes as they pass through the fishery while also protecting the stock against potentially harmful depletion when under the dominance of several weak year-classes. The problem of determining if, when, and how the algorithm should be applied is up to managers of the resource.

The model indicates that managing the Pacific whiting fishery according to MSY under a constant yield quota would allow at most 175 kt. Higher quota levels would lead to a stock crash over the long run. However, the analysis presented herein indicates that if managers are willing to adjust quotas on a year-to-year basis, a rather significant improvement in both average yield and average efficiency of removal (CPUE) can be attained. For example, a run of the algorithm at 400/400 results in expected yield of 178 thousand metric tons and a mean CPUE of 23.2 t/vessel-day (see Table 3).

The results of this analysis strengthen the justification for using a probabilistic rather than a deterministic treatment for modeling the whiting. First, we can compute variance of yield and stock which allows the consideration of the effect of the large variability associated with recruitment on yield and stock. We were not tied in this analysis to any predetermined stock–recruit curve form but are simply reflecting the effect of variability of the (albeit scanty) stock–recruit data on whiting population dynamics at various fishery levels. Finally, the probabilistic treatment allows us to consider risk explicitly by gearing policy algorithm decisions toward minimizing the risk of falling into a reduced stock condition. This can be represented by ensuring that the probability the stock is in the lowest discrete range is less than some predetermined level. (This can be used as an alternative to the present lower stopping rule which is based on expected stock level.)

The computational modifications in the model, including the "pairs" algorithm and the linear interpolation and smoothing of probability between adjacent ranges, has made analyses of fish and other animal stocks with large numbers of age-classes possible. The addition of the yield quota management feature and embedding the model within the policy algorithm presented above has enhanced the flexibility of the model for dealing with real fishery management problems subject, of course, to present data limitations.

Our analysis of the whiting fishery indicates that further analyses need to be undertaken, especially a sensitivity analysis of model behavior and of the policy algorithm solutions. We found that the variances in yield and stock level are quite sensitive to the maximum fecund stock biomass. It would also be informative to investigate the sensitivity of solutions to the transition matrix probabilities, especially in the region below observed stock levels, to the age of maturity, and to the catchability coefficients. To consider interactions between parameters without an inordinate number of model runs, a fractional factorial design would have to be used (Rose and Swartzman 1981).

Our approach could also be usefully applied to other fisheries having highly variable recruitment such as the Pacific halibut and king crab fisheries. Also, the approach could be extended to include additional socioeconomic aspects in the analysis, such as capitalization and depreciation costs in the fishery and the sociological implications of variable annual effort levels.

Acknowledgments

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Appendix A

DEFINITION OF SYMBOLS

BDS(J)	The base decision sequence after J iterations of the policy algorithm gives trial effort levels over the next 5 yr
c_i	Fraction of sexually mature fish in age-class i
$E(\cdot)$	Expected value (mean) of argument
i	Age-class index ($i = 1, \ldots, n$)
ISW	Switch in policy algorithm denoting that expected stock is above SR_u after the previous iteration of the policy algorithm
j	Index of subdivision of population numbers in each age-class for the discrete probability distribution ($j = 1, \ldots, m$)
J	Number of iterations of the policy algorithm in a particular year
j_s	Index of subdivision of stock biomass levels for the discrete probability distributions ($j_s = 1, \ldots, m_s$)
JSW	Switch denoting stock is below SR_L after the first iteration of the policy algorithms
k	Index for time in integer years
K'	Number of levels for the pairs algorithm
KSW	Switch denoting stock is below SR_u after the first iteration of the policy algorithm
m	Number of subdivisions for age-class distributions
m_s	Number of subdivisions for adult stock biomass discrete distribution
n	Number of age-classes in the model
$\mathbf{P}_i(k)$	Vector of probabilities (discrete probability distribution) for population levels in age-class i at time k
$p_{ij}(k)$	The jth element of $\mathbf{P}_i(k)$ above
$\mathbf{P}_s(k)$	Vector of probabilities (discrete probability distribution) for adult stock biomass levels at time k
$p_{sj}(k)$	The jth element of $\mathbf{P}_s(k)$
q_i	Catchability coefficient for age-class i
r	The age at which a fish cohort is recruited to the fishery
s	Fecund stock biomass level (metric tons)
$\hat{S}$	Maximum fecund stock biomass level (metric tons)
$S_d(k)$	Desirable stock in year k, i.e. all adult whiting age 5 and older
SR_L	Lower stopping rule — level above which we want to maintain the stock at all times in the policy algorithm
SR_u	Upper stopping rule — level above which we desire stock to be after 5 yr in the policy algorithm
t_s	Time spawning season begins as a proportion of the year that has passed, i.e. $0 \leq t_s < 1$
t'	Time in years in the policy algorithm $t' = 1, \ldots, 5$
$\bar{t}$	$(0, \bar{t})$ is the portion of each year that is open to fishing
t_{lj}	Denotes the probability that stock biomass level j will give rise to recruits r yr later at recruit level l
$\mathbf{T}$	Stock–recruitment transition matrix of elements t_{lj} ($l = 1, \ldots, m$ and $j = 1, \ldots, m_s$) (see above)
$V(\cdot)$	Variance of arguments
$v(k)$	Fishing intensity over time
v_k	Constant fishing intensity during year k
v_0	Initial effort level for the next 5 yr in the policy algorithm
w_i	Average biomass of an individual fish in age-class i

$\hat{x}_i$	Maximum number of fish in age-class i
$Y(k)$	Yield in year k (a random variable)
ΔSR_u	Change in SR_u after each iteration when stock is below SR_u in policy algorithm
Δv	Increment or decrement in effort for each iteration of the policy algorithm
ΔV	Change in base decision sequence = (Δv, Δv, Δv, Δv, Δv)
$\Delta V'$	Change in base decision sequence = (0, Δv, Δv, Δv, Δv)
α_i	Natural mortality for age-class i

Appendix B

Discussion of Modifications to the Getz–Swartzman (1981) Model

As mentioned earlier, the pairs algorithm improved the running speed of the model and allowed having a larger number of age-classes without significant increase in run time. The algorithm computes the fecund stock biomass probability vector from the age-class biomass probability vectors by adding the age-classes in pairs (instead of all at once as in Getz and Swartzman 1981). The algorithm takes $n/2$ pairs of vectors at the first level and puts each of them into $2m$ ranges. For example, the probability vectors for age-class i and $i+1$ are "added" to form a probability vector with $2m$ ranges between 0 and $\hat{x}_i w_i c_i + \hat{x}_{i+1} w_{i+1} c_{i+1}$. At the second level, $n/2$ probability vectors having $2m$ ranges are added in pairs to produce $n/4$ probability vectors having $4m$ ranges. This continues until only one pair of probability vectors is left and these are added to produce the stock biomass probability vector. (There are m_s stock biomass ranges between 0 and $\hat{S}$.) The total number of levels necessary, K', depends on the number of age-classes n and is the integer such that $2^{K'-1} < n \leq 2^{K'}$. To account for the fact that the number of pairs may not be an even power of 2, the algorithm creates null probability vectors (vectors with zero maximum values and having a probability 1 of being in any of the ranges) to bring the total number of vectors to an even power of 2. The additional vectors do not change the stock level computed. We found this preferable to keeping track of the number of pairs explicitly in the algorithm as so many special cases were then involved. The pairs algorithm represents an approximation to the original stock algorithm. We found differences of less than 10% in stock probabilities between stock probabilities calculated using the pairs algorithm and the calculations using the original algorithm.

A smoothing algorithm involving linear interpolation of probabilities was developed to reduce instabilities in combining probabilities resulting from discretization of the stock and age-class ranges. The interpolation was accomplished by spreading probabilities between two adjacent ranges depending on how far from and which side of the midpoint of the range a probability fell into. Thus, if in adding the nominal values of two ranges the sum fell on the midpoint of a range (in the vector representing the sum of the two original vectors) all probability went into that range. If it fell on the boundary between two ranges, half went to each range. A linearly increasing portion of the probability fell within a range as the sum of the nominal values fell closer to the midpoint of that range.

After incorporation of the linear interpolation and smoothing in computing stock, we found that several minor stability problems we had encountered in long-term runs of the model disappeared and particularly that curves of equilibrium yield (obtained from long-term runs of the model at constant effort) against effort were smoothed out at high effort levels rather than going up and down as they had previously.

NOTES

An Effective Method for Tagging Marine Polychaetes

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JOULE, B. J. 1983. An effective method for tagging marine polychaetes. Can. J. Fish. Aquat. Sci. 40: 540–541.

Two commercially harvested marine polychaetes, *Glycera dibranchiata* and *Nereis virens*, were successfully tagged with coded microwire tags placed in the coelomic cavity. Mortalities incurred during the experimental periods appear to be subject to the animals' sensitivity of being held under laboratory conditions rather than the tagging procedures. Average tag retention for the experiment was 82% among survivors.

JOULE, B. J. 1983. An effective method for tagging marine polychaetes. Can. J. Fish. Aquat. Sci. 40: 540–541.

Deux polychètes marins d'importance commerciale, *Glycera dibranchiata* et *Nereis virens*, ont été marqués avec succès à l'aide d'un microfil métallique codé placé dans la cavité coelomique. Les mortalités qui se produisirent durant les périodes expérimentales semblent causées par la stabulation des animaux dans des conditions de laboratoire plutôt que par le marquage lui-même. En moyenne, la rétention des marques a été de 82 % parmi les survivants de l'expérience.

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NO suitable techniques for marking soft-bodied invertebrates have been reported although these could be of considerable aid for studies of biology and population dynamics. For example, the commercial harvesting of at least two species of marine polychaetes in Maine has led to management research involving their population dynamics (Creaser 1973). Several methods of marking marine worms have been explored but with little success. Adhesives, paints, dyes, and radioactive substances were tested by Gustafson (1953), who reported variable, but generally unsatisfactory, results. Scarring with silver nitrate was attempted by Klawe (1954) but this too shared in the lack of permanence that plagued the other marking techniques.

Coded microwire tags were developed for tagging fish and have been used on Pacific salmon (*Oncorhynchus* sp.) (Jefferts et al. 1963) and herring (*Clupea harengus*) (Corten 1980). Microwire tags have also been used for invertebrates including American lobster (*Homarus americanus*) (Ennis 1972) and prawns (*Pandalus platyceros*) (Prentice and Rensel 1977). These tags are advantageous for marking small animals because they are small, readily implanted, and can be detected without killing the animals. My objective was to determine the feasibility of tagging bloodworms (*Glycera dibranchiata*) and sandworms (*Nereis virens*) with coded magnetic microwire tags.

Materials and methods — The coded microwire tags were made of magnetic, biologically unreactive type 302 stainless steel wire (manufactured by Northwest Marine Technology (NMT) of Shaw Island, Washington), 1.07 mm in length and 0.25 mm in diameter. Each tag was injected with a 24-gauge hypodermic needle attached to a syringe equipped with a push rod to eject it. Detection of tags was accomplished with an NMT magnetic field detector.

Juvenile through adult size worms collected from intertidal mud flats in the vicinity of Wiscasset, Maine (69°40′W; 44°00′N) were acclimated to laboratory conditions by holding them in floating trays held in a flow-through seawater system (2.9–3.9°C, 30.4–31.2‰) at the Maine Department of Marine Resources laboratory at West Boothbay Harbor, Maine.

To test tag retention, I held worms either in floating trays or in a simulated mud flat environment. The floating trays were fabricated of wood with 1-mm dacron-mesh bottoms to permit free circulation of water. To simulate the mud flat environment, I collected undisturbed sections of intertidal mud (20 × 22 × 39 cm) from a mud flat near the sampling site. I removed these sections from the flat using a rectangular sheet steel cutter and placed them in trays submerged in 500-L flow-through seawater tanks. The mud was held for 7 d before the worms were introduced.

Three groups of bloodworms and sandworms were used for each experiment. The first experiment, in which worms were

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held in running seawater, consisted of 50 worms that were injected with tags, another 50 bloodworms and 41 sandworms (unfortunately 9 other worms escaped during acclimation) were injected without the insertion of tags, and a control group of 50 untreated worms. The tags were inserted in the anterior coelomic cavity between the 10th and 20th segments. I chose this location because the anterior coelomic cavity is larger than the gut thus improving the chance of proper tag placement, and because injured worms, especially sandworms, have a tendency to shed the posterior portion of the body. After treatment, the 50-worm groups for both bloodworms and sandworms were placed in the holding trays.

The magnetic detector was used to ascertain tag implantation in the worms immediately after treatment. To assure uniformity of handling, the other two groups for both species were also passed through the detector. The worms were held in the trays for 2 wk and checked daily for mortalities. At 5-d intervals, they were checked for tag retention. After 2 wk, the tagged worms were placed in the mud-filled holding tanks and held for 7 wk, at which time they were reexamined for tag retention.

The second experiment for both sandworms and bloodworms shared an identical protocal except that 25 worms were used in each group, and these were placed directly in submerged mud trays after treatment. After 10 wk, I retrieved the worms and checked them for tag retention. In this experiment, tank outlets were screened to prevent escape of worms; missing animals were recorded as mortalities.

Results and discussion — Tag retention after 2 wk in the floating trays was 86% ($n = 39$) for the bloodworms and 84% ($n = 42$) for the sandworms in the first experiment. All sandworm tag losses occurred within the first 5 d, as did most of the tags lost by bloodworms. Mortalities during the 2-wk holding period were five (10%) for tagged bloodworms, two (4%) for injected but untagged bloodworms, none for the bloodworm control group, one (2%) mortality for the control group of sandworms, and none for the other two sandworm treatment groups. After the 10-wk experiment, the final results were 84% ($n = 38$) tag retention for the tagged bloodworms, 84% ($n = 42$) tag retention for the sandworms, and no further mortalities. In the second experimental procedure, tag retention for the bloodworms was 81% ($n = 17$) and 80% ($n = 20$) for the sandworms. The only mortalities incurred during this 10-wk period were found in the bloodworm group, four (16%) for the tagged group, nine (36%) for the injected but untagged group, and five (20%) for the control group.

Mean tag retention among survivors for all tagged groups was 82%. The greatest incidence of tag loss occurred within the first 5-d period. I attributed this to misplacement of the tag in the gut rather than in the coelomic cavity; consequently, the tags were eliminated with the fecal pellets. This problem could be avoided by holding the worms for several days after injection and then checking them with the detector to cull any untagged individuals. Injection and tag placement did not cause any noticeable damage to the organisms. Sandworms survived better than the bloodworms in both the floating trays and the mud trays as reflected in the mortality results. From observations made while detecting tagged individuals, it appears the tags did not move around in the coelomic cavity. The use of floating trays allowed easy examination of the worms; this is important because retrieval from mud is difficult and often results in injuries. Tagged and untagged individuals are easily differentiated when passed over the detector. I conclude that this is a viable method for tagging polychaete worms. Moreover, it will facilitate studies of growth and movement.

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Measurements of Dissolved Adenosine Triphosphate in Lake Michigan[1]

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Comparisons of two methods of separating dissolved adenosine triphosphate (dATP) were made, both in the laboratory and in vertical profiles in Lake Michigan. Laboratory work indicated that filtration through a 0.2-μm pore filter or centrifugation of samples gave similar concentrations of dATP. In Lake Michigan, however, the filtration method gave significantly higher dATP concentrations suggesting some adverse filtration effect. Therefore, centrifugation was chosen as the method to determine dATP. Resulting particulate ATP (pATP) concentrations indicated the highest levels of microbial biomass were located below the epilimnion. Feeding by *Mysis relicta* appeared to decrease pATP but not release much dATP.

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Nous comparons deux méthodes de séparation de l'adénosine triphosphate dissoute (dATP), à la fois en laboratoire et dans des profils verticaux du lac Michigan. En laboratoire, on constate que la filtration à travers un filtre à pores de 0,2 μm et la centrifugation des échantillons donnent des concentrations de dATP identiques. Par contre, dans le lac Michigan, les concentrations de dATP déterminées par filtration sont nettement supérieures, ce qui laisse supposer quelque effet défavorable de filtration. Nous avons donc opté pour la centrifugation comme méthode de dosage de dATP. Les concentrations de ATP particulaire (pATP) ainsi obtenues indiquent que les niveaux maxima de biomasse microbienne sont situés au-dessous de l'épilimnion. L'ingestion par *Mysis relicta* semble réduire la pATP, mais ne libère pas beaucoup de dATP.

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SINCE the initial description of a methodology for the analysis of adenosine triphosphate (ATP) in aquatic samples (Holm-Hansen and Booth 1966), many changes in various aspects of this technique have been proposed and used (see review by Karl 1980). One of these changes was the development of direct extraction of samples which gave investigators greater concentrations of ATP when compared to filtered extractions (Azam and Hodson 1977b; Jones and Simon 1977). Azam and Hodson (1977b) suggested that these higher measurements of ATP with direct extractions could have been caused by cell-free ATP.

The presence of dissolved ATP (dATP) and its breakdown by aquatic bacteria has been demonstrated in both marine (Azam and Hodson 1977a; Hodson and Azam 1977; Hodson et al. 1981a, b) and freshwater (Riemann 1979) environments. These reports of dATP confirmed the observations of Koenigs and Hooper (1973), who found dissolved mono-, di-, and tri-phosphate nucleotides while investigating organic phosphorus compounds in a Michigan bog lake. Several methods for separating dATP from total ATP (tATP) have been used, including filtering samples through a 0.2-μm pore filter to remove particulate ATP (pATP) (Azam and Hodson 1977a; Riemann 1979) and by centrifuging the sample (Jones 1979).

One possible source of dATP in the water column is phytoplankton mortality due to zooplankton grazing (Azam and Hodson 1977a; Riemann 1979). In Lake Michigan during summer stratification, a subthermocline chlorophyll maximum occurs (Brooks and Torke 1977; Bowers 1980). The opossum shrimp, *Mysis relicta*, nocturnally migrates to this maximum in large numbers and feeds (Beeton 1960; Bowers and Grossnickle 1978; Grossnickle 1979).

Our objective was to compare the above methodologies for separating dATP from tATP in the laboratory and the field and to examine the possible role of feeding by *M. relicta* on dATP and pATP concentrations in Lake Michigan.

Methods and materials — The sodium salt of ATP (Sigma Chem. Co., St. Louis) was used for laboratory studies. It was dissolved and diluted to a concentration of 10 μg ATP·L^{-1} using autoclaved double-distilled water. To determine if the separation techniques would be comparable in recovering dATP, subsamples were treated in the following manner:

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TABLE 1. Recovery of ATP from laboratory extractions with an initial concentration of 10 $\mu g \cdot L^{-1}$.

Treatment	Extraction temperature	Recovery ATP (μg/L) 1	2	avg.	% difference in recovery
1. tATP	Hot	6.12	6.33	6.22	3.2
2. F-dATP	Hot	5.01	5.82	5.42	13.9
F-dATP	Cold	6.12	6.30	6.21	2.8
3. C-dATP	Hot	5.52	5.22	5.37	5.3
C-dATP	Cold	6.22	6.01	6.13	3.3

1) A 1.0-mL subsample was extracted in 4 mL of boiling Tris buffer (0.02 mol/L, pH 7.75) over a bunsen burner to measure tATP (Jones and Simon 1977) (tATP).

2) A 20.0-mL subsample was filtered through a sterile Nuclepore filter (0.2 μm pore size, 47 mm diameter) at low vacuum (pressure differential ≤ 4 cm Hg) into a sterile glass bottle (after Riemann 1979) (F-dATP).

3) A 20.0-mL subsample was placed in a sterile test tube and centrifuged for 15 min at low speed (75 g). The top 50% of the water was carefully removed, placed in another sterile test tube, and centrifuged at a higher speed (330 g) for 15 min (after Jones 1979; and J. G. Jones, Freshwater Biological Association, personal communication) (C-dATP).

Extractions for dATP were made from the final filtrate of 2 and out of the top 50% of the final supernatant of 3. Jones (1979) suggested that if dATP in water is a true solution of the molecule, then extraction with boiling should not be necessary, so dATP extractions were made by placing 1.0 mL into 4 mL of boiling Tris buffer as in 1, and by taking 1.0 mL and placing it in room temperature Tris buffer (0.02 mol/L, pH 7.75). All extractions were made in duplicate and frozen until analysis.

In the field, samples were collected at a series of deep stations (100 m) in Lake Michigan, ~27 km northeast of Milwaukee, WI, during an overnight cruise July 17–18, 1980 on the R/V *Neeskay*. Vertical profiles of temperature and ATP concentration were taken at 17:30 under daylight conditions on July 17, 1980 and at 01:00 with artificial lighting conditions and at 03:00 under normal darkness on July 18, 1980 (all times CDT). The last two sampling stations were 1–3 km apart. Artificial lighting consisted of a Boston whaler with eight automobile headlamps shining down into the water. This setup was based on the observations that bright moonlight inhibited ascent of *M. relicta* at night (Beeton 1960; Bowers and Grossnickle 1978) and that shining of bright lights on the water would also prevent ascent (Teraguchi et al. 1975). The last station was far enough away from the lighted station (~1.6 km) that *M. relicta* was not inhibited in its nocturnal ascent.

Water samples were collected with a clean 9-L PVC Van Dorn bottle and ~100 mL was placed in sterile glass bottles before extraction. Total ATP was extracted as in 1 of the laboratory study (Jones and Simon 1977), whereas dATP was separated as in 2 and 3 using boiling extractions only. All extractions were made in duplicate and were frozen until analysis.

All centrifugations in both the laboratory and the field were performed using an IEC clinical centrifuge (Damon/IEC Division, Needham Hts, MA). Tris buffer (0.02 mol/L, pH 7.75) for all extractions and standards was made according to Strickland and Parsons (1972).

Light emission to determine both tATP and dATP was measured in an Aminco-Chem-Glow ATP photometer interfaced with an Aminco integrator timer and a strip chart recorder. The enzyme mixture was made according to Jones and Simon (1977) using crude firefly lantern extract (FLE-50, Sigma) and added luciferin. The sample to enzyme ratio used was 2:1, the same as Jones and Simon (1977), but with 400-μL and 200-μL volumes used instead of 266-μL and 133-μL. The enzyme preparation was injected into samples using an automatic syringe (Jones and Simon 1977). To avoid interference by other nucleotide phosphates (Karl 1978; Riemann 1978; Stevenson et al. 1979), all ATP measurements were made with a 0- to 5-s integration of the peak height. Samples were analyzed and compared to reagent blanks and a series of ATP standard solutions to quantify the levels of tATP and dATP.

Data from the different extractions in the laboratory and the field were separately analyzed using both paired and unpaired *t*-tests and one-way analysis of variance (ANOVA) (Zar 1974).

Results — The recovery of ATP from the extraction procedures in the laboratory is presented in Table 1. Duplicate extractions yielded recoveries within 10% of each other except for the F-dATP hot extraction. All extractions [(1) tATP, (2) F-tATP hot and cold, (3) C-dATP hot and cold] were not significantly different from each other (*t*-tests, $P > 0.05$).

Vertical profiles of tATP, F-dATP, C-dATP, and temperature from the stations in Lake Michigan are displayed in Fig. 1. All pairs of tATP extractions were within 10% of each other, as were all pairs of F-dATP extractions. Most pairs of C-dATP extractions were within 10% of each other except for 30 m, 17:30 (within 17%), and 20 m, 03:00 (within 12%). In the three vertical profiles, tATP ranged from 183 to 783 $ng \cdot L^{-1}$ with the highest concentrations occurring in metalimnetic waters. Secondary peaks were observed under the thermocline. F-dATP ranged from 44 to 250 $ng \cdot L^{-1}$ and constituted from 8.4 to 82.9% (average = 40.1) of corresponding tATP concentrations (Table 2). C-dATP ranged from 2 to 129 $ng \cdot L^{-1}$ and, similar to tATP, maximum levels were observed in metalimnetic waters. C-dATP constituted from 0.8 to 25.9% (average = 12.1) of the corresponding F-dATP concentrations (Table 2).

Filtration yielded significantly different concentrations of

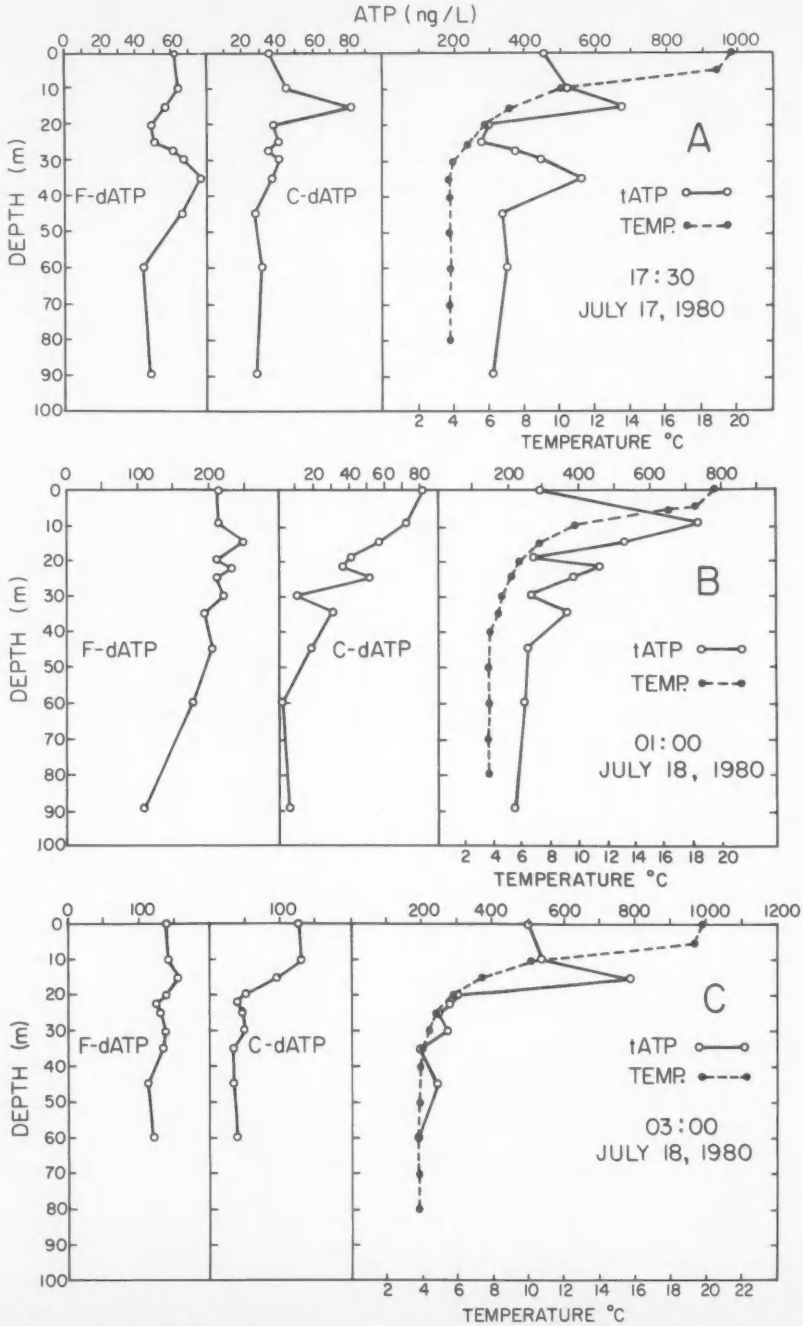

FIG. 1. F-dATP, C-dATP, tATP, and temperature vertical profiles in Lake Michigan. (A) 17:30 on July 17, 1980 (daylight conditions). (B) 01:00 on July 18, 1980 (artificial light conditions). (C) 03:00 on July 18, 1980 (normal darkness).

TABLE 2. (A) F-dATP and (B) C-dATP expressed as percentages of tATP, and (C) C-dATP expressed as a percentage of F-dATP at the same time and depth.

	17:30, July 17, 1980			01:00, July 18, 1980			03:00, July 18, 1980		
Depth (m)	A	B	C	A	B	C	A	B	C
1	13.7	7.9	58.0	68.1	25.9	37.9	27.6	24.6	88.9
10	11.1	7.9	71.8	29.3	9.8	33.3	26.2	24.3	92.8
15	8.4	12.1	143.8	47.8	10.9	22.8	19.5	12.0	61.4
20	16.7	12.9	77.5	78.9	15.2	19.2	46.7	16.8	33.0
22	nd[a]	nd	nd	50.9	8.3	16.2	44.2	12.9	29.2
25	18.7	15.0	80.4	55.4	13.3	23.9	52.7	17.1	32.5
27	16.5	9.6	58.0	nd	nd	nd	nd	nd	nd
30	15.1	9.2	61.2	82.9	3.7	4.4	50.4	17.2	34.1
35	13.7	6.7	49.3	54.0	8.6	15.9	69.6	16.2	23.3
45	19.9	8.3	41.8	81.7	7.1	8.7	46.8	13.1	27.9
60	12.6	8.8	70.4	73.4	0.8	1.1	65.6	20.8	31.6
90	15.7	8.9	51.1	50.2	3.2	6.3	nd	nd	nd

[a]nd, no data.

dATP than centrifugation in the whole water column at each time period (paired t-test, $P < 0.05$). The samples from the water column were divided into epilimnetic (surface to 5 m), metalimnetic (5−20 m), and hypolimnetic (20 m and down) categories to test where the differences occurred. At 17:30 significant differences existed between F-dATP and C-dATP treatments in the epilimnion and hypolimnion (ANOVA, $P < 0.05$), but not in the metalimnion (ANOVA, $P > 0.05$). At 01:00, F-dATP and C-dATP were significantly different in the epilimnion, metalimnion, and hypolimnion (ANOVA, $P < 0.05$). At 03:00, F-dATP and C-dATP were not significantly different in the epilimnion (ANOVA, $P > 0.05$) but were significantly different in the metalimnion and hypolimnion (ANOVA, $P < 0.05$). At each sampling time, F-dATP concentrations were significantly different from those at other time periods (unpaired t-tests and ANOVA, $P < 0.05$). C-dATP data showed no significant differences between results at different sampling times (unpaired t-tests and ANOVA, $P > 0.05$).

Discussion — In the laboratory experiment, both the filtration method [(2) F-dATP] and the centrifugation method [(3) C-dATP] yielded similar results indicating that no inherent differences existed between the methods when only dATP was involved. Furthermore, no significant difference was found between hot and cold extractions of these two methods, supporting the premise (Jones 1979) that if dATP is a true solution, then boiling extractions should not be necessary.

In the field, the two methods gave significantly different results which appeared throughout the water column under artificial lighting (01:00) but not under natural conditions (17:30 and 03:00). F-dATP concentrations were usually higher than corresponding C-dATP concentrations as had been previously reported by Jones (1979). In our studies, F-dATP yielded a wider range of tATP (range = 8.4−82.9% of tATP) than Jones (1979) observed (range = 25.28% of tATP) and appear closer to the data reported by Riemann (1979) in his investigation of eutrophic lakes (range = 14−76% of tATP). C-dATP average percentages of both tATP (40%) and F-dATP (43.9%) compared well with percentages reported by Jones (1979) (25−28% and 40−60%, respectively).

TABLE 3. Vertical distribution of pATP (ng/L) in Lake Michigan at the three sampling times.

Depth (m)	17:30 (July 17)	01:00 (July 18)	03:00 (July 18)
1	415	235	371
10	472	665	402
15	596	466	689
20	256	229	242
22	nd[a]	421	242
25	232	333	198
27	340	nd	nd
30	402	260	222
35	524	330	160
45	309	234	207
60	319	243	145
90	284	212	nd

[a]nd, no data.

The difference between the results in the laboratory and the field suggest that other factors are involved in the field besides dATP which contribute to the higher concentrations in the F-dATP. Although some bacteria are able to pass through 0.2-μm pore filters (Hobbie et al. 1977; Zimmermann 1977), it is doubtful that the centrifugation used in this study would completely remove them. They may contribute partially to the difference. Filtration effects have been reported for ATP extractions (Sutcliffe et al. 1976; Jones and Simon 1977; Karl and Holm-Hansen 1978). Karl and Holm-Hansen (1978) reported a decrease in the normalized total amount of ATP with increase in the volume filtered, but observed no differences in total adenylate concentration and concluded that filtration stress results in a rearrangement of cellular adenine nucleotides and not cell lysis. However, Jones and Simon (1977) and Jones (1979) filtering only 1 mL (compared to 20−500 mL by Karl and Holm-Hansen 1978) found a loss of ATP by filtration which they felt was greater than could be explained by changes in energy charge alone and suggested cell lysis may be occurring. Certainly in the data from Lake Michigan, filtration appears to result in some effect on dATP

concentrations, so to avoid these effects we have chosen the C-dATP as representative of dATP in Lake Michigan. Subtracting C-dATP from tATP reveals the vertical distribution of particulate ATP (pATP) in Lake Michigan (Table 3). The chlorophyll *a* maximum in the lake during stratification is found under the thermocline (Brooks and Torke 1977). We observed maximum levels of pATP in metalimnetic waters along with some subthermocline peaks. This indicates that the highest levels of microbial biomass were located below the epilimnion.

"Sloppy feeding" by zooplankton on algae has been proposed as a source of dATP in natural waters (Azam and Hodson 1977a; Riemann 1979; Karl 1980). Support for this arises from the work of Lampert (1978), who showed that up to 17% of the algal carbon ingested by *Daphnia pulex* could be lost as dissolved organic carbon from algae damaged during feeding. *Mysis relicta* in Lake Michigan has been observed to fragment large algal filaments while feeding (Bowers and Grossnickle 1978), and in laboratory experiments from 1 to 3% of the organic carbon removed from suspension by *M. relicta* during the 1st hour of feeding on cultured diatoms (*Fragilaria* sp.) was lost from damaged cells (Sierszen and Brooks 1982). Examination of the pATP revealed that a subthermocline peak which was present at 17:30 was no longer observed at 03:00 suggesting that feeding by *M. relicta* may have been responsible for its decrease. However, there was no significant increase at 03:00 in C-dATP from either 17:30 or 01:00 with artificial light which may mean that *M. relicta* is a relatively efficient feeder. This is supported by the low release of dissolved organic carbon by feeding *M. relicta* reported in the laboratory (Sierszen and Brooks 1982).

From the preceding discussion it should be apparent that the choice of method for dATP determination has implications upon the conclusions drawn. Because investigators have shown that dATP is a source of utilizable carbon for aquatic bacteria (Azam and Hodson 1977a; Riemann 1979; Hodson et al. 1981a, b), the accurate determination of in situ levels of dATP is important for determining natural uptake rates. We recommend that experimenters examine carefully the method chosen to measure dATP. Based on our data, we chose centrifugation as in the field all filtration affects could be avoided. We also agree with Karl (1979), who cautioned against the use of direct extraction techniques with aquatic samples unless corrected for dATP. The choice of method for determining this correction will also influence the amount of particulate ATP found.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on Perspective: Ocean Sciences in Relation to Living Resources

A recent Perspective in this *Journal* (Bakun et al. 1982) included the text of a report on this subject which most readers will have interpreted as being the output of a Working Group established by SCOR and ACMRR in response to a request by IOC, and the article appears to have been drafted with this intention.

In fact, this is not the case. The article is based on the report of a group of consultants to the staff of FAO Fisheries Branch, on the same subject, prior to the establishment of the formal SCOR–ACMRR Working Group No. 67 under the chairmanship of R. Barber. The report of Working Group No. 67 was submitted formally to IOC at the Twelfth Session of the Assembly, and adopted by that body as Resolution XII-1 in the terms given below (Appendix). Although we do not disagree with the scientific content of the Bakun–Beyer–Pauly–Pope–Sharp report, which is an excellent review of a difficult subject, we wish to avoid confusion between the two reports. IREP, the International Recruitment Programme, arising from the report of Working Group No. 67 and adopted by IOC as part of their program, is surely destined to become a familiar part of international biological research; it will be unfortunate if its objectives are obscured as a result of the manner in which the internal FAO consultants' report was published — ALAN LONGHURST, *Secretary, Scientific Committee on Oceanic Research, Bedford Institute of Oceanography, Dartmouth, N.S., Canada* AND GOTTHILF HEMPEL, *Chairman, FAO Advisory Committee on Marine Resources Research, Alfred Wegener Polar Research Institute, Bremerhaven, FRG.*

Appendix

Resolution XII-1

OCEAN SCIENCE IN RELATION TO LIVING RESOURCES (OSLR)

The Intergovernmental Oceanographic Commission,

A

Recalling Resolution XI-17 approving the development by the Commission of a Programme of Ocean Science in Relation to Living Resources (OSLR),
Expresses its appreciation to SCOR and ACMRR for the report of their joint Working Group No. 67 (Document IOC-XII/8 Annex 1a) which was submitted to the Assembly in response to the Commission's request for advice on this Programme;
Adopts OSLR as a new scientific programme of the Commission.

B

Agreeing with the SCOR view that the first major objective of the Commission's OSLR Programme should be to gain a better understanding of the effect of environmental conditions on recruitment of fish stocks, this being one of the central and long-standing but still largely unresolved problems in marine science in relation to living resources,
Noting that progress towards this objective would be of direct assistance to Member States in their task of achieving the best management of fish resources and in support of FAO activities to that effect,
Acknowledging that the multi-disciplinary research involved is particularly demanding logistically and calls for the concerted application of a wide range of scientific skills, together with the necessary facilities, at sea and ashore, on a long-term basis,
Agreeing also with the conclusion of SCOR/ACMRR Working Group No. 67 that a promising approach would therefore be to develop an international programme comprising a network of investigations into the relevant aspect of the quantitative ecology of selected fish species, co-ordinated in space and time and using similar techniques (hereafter called the International Recruitment Project, IREP),
Noting also that one possible form that this programme could take is that described in the report of the SCOR/ACMRR Working Group No. 67 as IREX (International Recruitment Experiment),
Being aware that much consultation and detailed planning will be required before such an international programme can be undertaken,
Invites the FAO to co-sponsor the OSLR Programme and the International Recruitment Project in particular;
Establishes a Guiding Group of Experts on the OSLR Programme, with the Terms of Reference contained in the Annex attached to this Resolution, and requests the Group to report on progress to the Executive Council at its Seventeenth Session;
Accepts with appreciation the offer from Canada to host a Workshop on the future planning of the IREP;
Accepts also with appreciation the offer from the Unesco Division of Marine Sciences to sponsor a working group to examine the special problems of high-diversity ecosystems in the context of the OSLR Programme.

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OBITUARY / NÉCROLOGIE

Francis Derwood McCracken
1916-1982

With the death of Frank McCracken on November 21, 1982, Canada lost a highly respected, dedicated, and successful scientist who had devoted a lifetime to research and problem-solving in Atlantic fisheries.

Frank McCracken was born in Roblin, Ontario, near Napanee, on September 30, 1916. He attended Queen's University and graduated in 1938 with an Honours B.A. in biology and chemistry. In the fall of 1938 he enrolled in the Ontario College of Education graduating in 1939 with a teaching certificate. Jobs were scarce in early 1939 but Frank was fortunate to find work in the Toronto offices of Canada Packers. In 1940 he obtained employment closer to home at the Aluminum Company of Canada, in Kingston, where he worked until joining the Canadian Army (Infantry) in 1943. His army career took him to British Columbia where he was stationed at war's end, learning Japanese in preparation for the impending assault on Japan.

He was discharged in January 1946 and in April began active fisheries work. He was hired as a temporary research assistant by the Fisheries Research Board to work at the St. Andrews Biological Station on Atlantic halibut. With the assistance of Dr A. W. H. Needler, then Director at St. Andrews, he entered graduate school at Toronto in the fall of 1946, using the halibut data as the basis for his research. In November 1946 he married Margaret ("Marnie") Edith McKeen, a young lady from Penticton, B.C., whom he had met during his army days in B.C. She was to be a lifelong companion.

His work on the ecology and growth of the Atlantic halibut in the Gulf of St. Lawrence earned him an M.A. degree from Toronto in 1947.

In May 1947 Frank was rehired as a summer research assistant at St. Andrews, this time to work on flounder investigations, which Dr Needler believed had sufficient scope and potential for a doctorate. Thus, in the fall he reentered graduate school at Toronto as a doctoral student under the supervision of Dr F. E. J. Fry. In May 1948 he again worked at the St. Andrews Biological Station, this time as a Senior Research Assistant. Finally, in January 1949, he was taken on permanent staff of the Fisheries Research Board of Canada as an Assistant Biologist for work in the groundfish program of the St. Andrews Station. From 1949 until 1954 he continued along that most difficult path — working full time, doing research for a Ph.D., and raising a family, all at the same time, for Marnie and Frank's two children were born during this period.

Frank was involved in groundfish investigations which were supervised by Dr W. R. Martin. Tagging programs for cod and halibut, halibut biology, groundfish bait research, and of course, winter flounder ecology were some of the areas of study. Finally after many interruptions, he was able to complete his graduate research at Toronto on the seasonal movements of the winter flounder, *Pseudopleuronectes americanus*, and received his Ph.D. in 1954.

Meanwhile, Frank had become interested in the problems associated with mesh-size efficiency in trawl nets and indeed became a recognized authority on mesh-size efficiency and regulation. Additional responsibilities at the Biological Station included life history studies, fish-tagging problems, management of the water laboratory, and research vessel design and replacement. It had become clear that there was a need for a research presence on the Scotian Banks, and Frank organized the first research vessel cruises using the M.V. *Harengus*, in 1958.

Throughout this early period he continued to work on groundfish research and from 1961 to 1967 served as Scientist-in-Charge of the program. In 1965, the program was expanded to include mollusks and gear research as well. In October 1967 he was appointed Assistant Director of the St. Andrews Biological Station, serving until 1971. As a

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result of his interest in mesh-size regulation he was a delegate at the 1963 FAO Fishing Gear Congress held in London, England.

The 1960s were busy and productive years. Since 1952 he had become increasingly involved with the International Commission for Northwest Atlantic Fisheries (ICNAF). He became an international authority in the field of mesh-size regulation for commercial trawling, primarily because of his extensive shipboard experience (which he loved) and his early recognition and interest in the problem. He continued to serve as a respected contributor and scientific advisor to ICNAF for over 20 yr. Even after retirement, he continued to provide assistance and advice on trawl mesh problems. In 1964 he was elected a Fellow of the American Institute of Fishery Research Biologists (AIFRB) for distinguished achievements in research and high ethical standards.

In the mid-1960s there was a move afoot to transfer the groundfish program to Halifax. The concept created much discontent in St. Andrews, particularly among the staff of the groundfish program which Frank headed. Fortunately, the proposed changes were not carried out.

About half of the total of 50 scientific papers published during his career appeared in the 1960s. These included studies of cod, halibut, argentine, winter flounder, redfish, and trawl nets, but studies of the haddock fishery predominated. The haddock studies involved age, growth, recruitment, onshore and offshore movement, and overall distribution in relation to season, depth, and bottom temperature.

In August 1969 he accepted a secondment to Ottawa to serve as a consultant to the Office of the Chairman of the Fisheries Research Board. His duties involved special consideration of Canadian scientific involvement in ICES and ICNAF and in the implementation of Atlantic programs for herring and salmon.

The tour of duty in Ottawa was to change Frank and Marnie's life most dramatically, for in February 1970, he suffered a major coronary attack and did not return to full-time work until June 1970. He continued his tour of duty in Ottawa and then returned to St. Andrews to continue his term as Assistant Director.

With the departure of Dr John Anderson to a Director General position in Ottawa in 1972, Frank took on the position of Acting Director of the St. Andrews Station. Effective January 1973, he again accepted an administrative position becoming Acting Atlantic Regional Director for Research, headquartered in Halifax, and responsible for three research stations in the Maritime Provinces, one in Newfoundland and general supervision of fisheries research vessels. He held this position until March 1974 when he became Scientific Advisor to Dr Bob Weir, the Chairman, Fisheries Research Board of Canada, and moved back to Ottawa. Following this Ottawa tour, the McCrackens returned to St. Andrews in April 1976, and after a few months at the Biological Station, Frank retired at the end of December 1976.

A dedicated and meticulous biologist, Frank continued to do consultative work for FRB — Fisheries and Oceans after retirement but the heart attack had left its mark and he could not maintain his former level of activity. For many years he was a keen and enthusiastic golfer, but he now had to take up walking a medically prescribed number of miles per day, often accompanied by his wife and constant supporter, Marnie. A quiet social life with much reading and the occasional winter trip south were the order of the day until the final attack in a Saint John Hospital. He is survived by his wife, daughter Joan, and son Paul. The memory of Frank as a quiet, friendly, and unassuming man with a rich background in fisheries science, which he willingly shared, will long remain in the minds and hearts of his many friends and colleagues at home and abroad.

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OBITUARY / NÉCROLOGIE

Frederick Ronald Hayes
1904–1982

Frederick Ronald Hayes was born in Parrsboro, Nova Scotia, in April 1904, and died in Halifax, September 1982. He attended schools in Parrsboro, Pictou, and Halifax and entered Dalhousie University for a degree in biology in 1922. While still an undergraduate, he was introduced by his teacher, Professor J. N. Gowanlock, to the St. Andrews Biological Station of what later became the Fisheries Research Board of Canada. His first scientific paper, on the periwinkle, was written there, under the inspiration and guidance of his mentor and of Dr A. G. Huntsman, the station director. His experience in marine biology and ecology under these two men was definitive, and after receiving his B.Sc. and M.Sc. from Dalhousie University in histology and embryology, he decided to take his Ph.D. degree in oceanography at the University of Liverpool. Unfortunately, soon after he arrived in England, his intended professor died, at which the young Hayes showed some of the versatility and adaptability which so characterized his future career. In 2 yr he completed a Ph.D. degree in chemical embryology! He then spent a year as a Rockefeller postdoctoral fellow at the University of Kiel before returning to Dalhousie University to replace Professor Gowanlock as professor of biology. There he met and married fellow biologist–professor Dr Dixie Pelluet, the Hayes family thus constituting two-thirds of the staff of the department. With the support of his wife, Ronald Hayes began the instruction of interested students in both laboratory and field on the physiology and ecology of salmon and their habitat.

During the wartime years, reduced staffs and increased demands meant extra workloads although, as was a repeated pattern throughout the life of Ronald Hayes, extraordinary challenges merely acted as stimulants. His clear mind and excellent memory coupled with an incisive wit and a flair for the Thespian Arts gave a growing audience of admiring and amused students the tools that promoted learning. Although his dedication to science and his high ideals for performance were widely appreciated, his relaxed manner provided little hint either of the strong sense of responsibility or the truly great labors involved in the tasks he set for himself. By 1946, however, the excellence of his efforts as teacher, researcher, and innovator were recognized in his election to Fellowship in the Royal Society of Canada. In 1948, in recognition of his major work in chemical embryology the University of Liverpool granted him the D.Sc.

Shortly after the war, wraps of secrecy were removed from the Chalk River Atomic Power Development. He was quick to recognize the potential of the new radioactive elements being offered for use in physiology and medicine as potentially powerful tools in ecology. As a consequence, he and his students performed classical experiments in limnology, for the first time introducing radiophosphorus into small lakes, detecting its initial rapid uptake in primary and secondary producers, and eventual deposition in the skeletons of fish and frogs.

Throughout his life Ron Hayes acted out the paradox of the committed individualist who nevertheless becomes one of the principal innovators and leaders of the organization of science both in his own University and in Canada. It was his firm conviction that the flow of the lifeblood of scientific discovery and development depended on the individual work of an elite of active and brilliant intellectuals. The essential task of universities was to find and foster these individuals and to teach them how to marshall the skills and effort required to complete both intellectual and practical undertakings. It was the necessary role of the other organizations of science to provide them with unstinting support. It was his own special talent to be able to keep in view the functions and new possibilities which the organizations and institutes could offer such individuals in a rapidly changing scientific scene. This, coupled with an intuitive sense of the needs of society for new biological knowledge, kept him at the head of his peers, urging and encouraging new developments and programs. In 1955, while

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head of the Department of Biology at Dalhousie University, he was appointed to the Fisheries Research Board of Canada (FRB), an appointment he retained for 10 yr until he accepted the invitation to become its full-time Chairman.

At about the time of his appointment to the FRB he began a remarkable exercise in creative imagination, patience, and both private and public diplomacy within the University that led to the creation in 1959 of a new interdisciplinary Institute of Oceanography and a new Division of Biological Sciences. These two organizations, of which he became founding Director and first Chairman, respectively, enabled Dalhousie University to offer its first and second Ph.D. programs, in oceanography and biology, respectively. In the same year he was appointed to membership on the National Research Council of Canada.

The move of Dalhousie University into scientific scholarship Hayes likened to the conversion of a "glorified English public school" into a real institution of higher learning. He directed his personal efforts to the guidance and growth of the institution into this sphere. The general acceptance of his view was signaled in 1963 when Dalhousie University created the post of Vice-President (Academic), which he was asked to fill. He believed that the post was evidence of a recognition by the University of a genuine new need in the surrounding society, and he accepted it as one way of supporting its commitment to meeting that need. For all his administrative experience, however, he was never able to think of himself as part of "the administration," continuing to suspect anyone who considered himself an administrator as in danger of becoming self-serving. He himself never lost the view that administration needed to be continually reminded that its function was to serve the needs of the community of scientists and scholars who were by definition dedicated to expose the natural and cultural truths needed by any civilized society. Throughout his life he seemed genuinely unaware of how his own vitality and vision played such a large role in guiding students and colleagues towards realization of these possibilities.

By 1964, when he was invited to become Chairman of the Fisheries Research Board, he had already warned of the winds of change blowing in the scientific establishment. As he later put it in his book, *The Chaining of Prometheus: Evolution of a Power Structure for Canadian Science*, "In the decade since (1961), Canadian science has been kept continually on the couch, pouring out its thoughts to one committee of social diagnosticians after another. Probably the scientific endeavour of no other country has endured so much scrutiny." He saw in this growing and persistent examination a naive insistence on harmonizing the aims and ideals of individual scientific effort with a vaguely defined sense of national worth and national aim. It was as though a group of administrative diviners sought to find the source of the life of science by poring through the entrails of a dismembered corpse. He felt that the image of science as a complex living organism made up of many separate parts playing equally vital roles provided a perspective important for our time. The needs of this organism were in danger of being badly served by a group of new government officials whose limited point of view led them to try to remold it into their own primitive image of a business, in which exchanges are mere buy–sell transactions between specialists interested in only their own welfare.

The view of science as an organism helped place many other institutions in their rightful setting. Universities, for example, were not merely generative mechanisms, but a seat of transformation of the energies needed to motivate the organism towards larger truths and finer performances. He saw, none the less, that the new officialdom was not about to show that confidence in universities which would permit them to play a role in policy developments in the real world of programs, plans, and budgets. It soon became equally clear to him that even the relative independence of government research boards like the Fisheries Research Board, the Defence Research Board, and the National Research Council made them suspect. To the world of business accountancy created by the Glassco Commission, there was only one board that could be trusted and that was Treasury Board!

Under the circumstances there was some urgency in demonstrating the constructive role of these scientific research institutions. In their capacity as centers of research, they must be able to show to what levels of excellence real efforts could lead. He turned his energies and talents to this end, both by creating new laboratories and in helping to forge new more active links among those already in existence. On the east coast he brought about the formation of the Marine Ecology Laboratory, the first laboratory of the Fisheries Research Board to have a mandate for research in basic production processes, thus creating an adjunct to his old Institute of Oceanography at Dalhousie, and a partner to the newly founded Atlantic Oceanographic Laboratory for the physical oceanographic sciences in Canada's new Bedford Institute of Oceanography. Similarly in Winnipeg, new links were formed between the University of Manitoba and the FRB Freshwater Institute, in St. Andrews, between the biological station and the Huntsman Marine Laboratory, and on the west coast between the Board's operations, the University of British Columbia, and the growing interests in Marine Sciences at the Universities of Victoria and Simon Fraser.

Ronald Hayes was not a man who concerned himself with retirement. When at age 65 his Ottawa appointment ended, he returned to Dalhousie University as a Killam Research Professor. There he began work on a number of publications dealing with development of science policy in Canada, most notably his incisive and witty *Chaining of Prometheus*, which besides its sharp portrayal of the inexorable swelling of science into large financial undertakings which invite the interventions of the budget directors and national planners, remains a paean to the potential selflessness and dedication of the best of individual scientists. It is a subject in which unsympathetic and unimaginative government administrators have found no humor whatsoever and Hayes recognized that his stance was perhaps a passing phenomenon. As he wrote, "Fortunately, so far, the university indoctrination that science candidates receive about the virtue of experimental truth has limited their predatory instincts. But the situation is unstable since no scientist likes to occupy indefinitely the position of court fool to the Treasury Board."

In typically constructive fashion he thereupon set to work upon the formation within Dalhousie University of an Institute of Environmental Studies. It was his perception that with the burgeoning of environmental concerns in government and

society generally, there was in this field of endeavor the need for independent perception and research that only the University could still supply. Completely undaunted by illnesses, he showed the customary diplomacy and vigor, and by 1974 succeeded in creating the new Institute involving cooperative actions not only by various departments and other institutions within Dalhousie, but forging links with Provincial government agencies and the Technical University of Nova Scotia as well. During this period, as founding Director of the Institute, he produced numerous briefs, and proposals, arranged meetings and contracts with government agencies, and organized groups of University professors to carry them out. In addition he initiated and participated in the teaching of a new graduate course and development of a degree program in Environmental Studies. The precariousness of his health and the sheer demands of the Institute forced him to resign the Directorship, although he continued first as assistant director and later as advisor and participant in courses and graduate supervision as his newest fledgling developed and grew into the Institute for Resource and Environmental Studies with teaching and degree-granting status within the Faculty of Graduate Studies.

He set a standard of effort and excellence for himself which it is difficult to understand and appreciate except in the presence of its living example. Some small reflection of it lives on in students who learned from him and colleagues who learned to admire both his style and the products of his remarkable vitality. The leadership he provided to the scientific and academic community through his wit and his vision are sorely missed.

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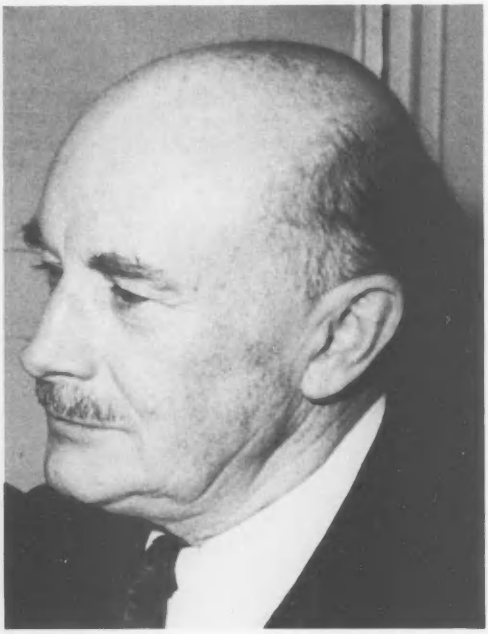
OBITUARY / NÉCROLOGIE

Donovan Bartley Finn, C.M.G.
1900–1982



Dr D. B. Finn, a name closely associated with fisheries research and development for a large part of this century, died in Rome in November, 1982. Dr Finn had lived in Italy since his retirement from the Food and Agriculture Organization of the United Nations (FAO), Rome, Italy, in 1964. Before joining FAO as Director of the Fisheries Division in 1946, Dr Finn had had an illustrious career as a fisheries scientist and administrator in Canada. He was the first Director of the Pacific Fisheries Experimental Station in Prince Rupert, B.C., in 1929; Director of the Halifax Technological Station in 1935; Chairman of the Salt Fish Board in 1939; and Deputy Minister of Fisheries from 1940 to 1946.

Dr Finn was born in London, England, in 1900. In 1912 his parents moved with their children to Canada. After a short stay in Brandon, Manitoba, the family settled in Winnipeg. As a boy of 15, Don Finn had to leave school and go to work. After a series of jobs he became relief operator for the Winnipeg Electric Railway. With a settled job he managed to continue his education and after passing entrance exams, he entered the University of Manitoba. He obtained a Bachelor of Science degree in 1924.

For the next 8 years Dr Finn continued to combine work and graduate studies. After a period as Associate Chemist with the American Cyanamid Company in Niagara Falls, Ontario, in 1924, he joined the Board's Technological Station in Halifax, N.S., under Dr Huntsman in 1925, and then moved to Prince Rupert in 1926. While there he obtained his Master of Science degree in 1928 from the University of Manitoba and became Director of the Station in 1929. It was under his leadership that the station's work program developed. He had a talented team which included Dr H. N. Brocklesby as Chemist, Dr H. C. Williamson as Zoologist, and Otto Young as Refrigeration Engineer. Dr Finn was also involved in his own research — he had became particularly interested in what happens to fish when they are cooled below the freezing point. In 1930 he went to Cambridge University in England and worked in the Low-Temperature Research Station under Sir William Hardy, and obtained his Ph.D. in 1932.

In 1935 Dr Finn returned to Halifax, N.S., this time as Director of the Station. In 1939 he was made Chairman of the newly formed Salt Fish Board, but his stay there was short-lived. While on a business trip to the West Indies, he received a cable from Prime Minister MacKenzie King, telling him to return immediately to take up the post of Deputy Minister of Fisheries in Ottawa.

The post of Deputy Minister had been vacant for some time and one of Dr Finn's first acts was to enlist the help of Dr Stewart Bates to build up the Department. As Deputy Minister Dr Finn was also Canada's Representative to the Fisheries Committee of the Combined Food Board. (The Board comprised Canada, U.K., and U.S.) This wartime Committee had the responsibility of recommending allocations of fish supplies and, in the case of salt cod, of recommending export prices. In 1946 Dr Finn was awarded the C.M.G. in recognition of his wartime work.

It was during this period that Dr Finn first became involved with international fisheries and the problems of fisheries development in what is now known as the Third World. He was a member of the Canadian delegation to the International Conference on Food and Agriculture convened by President Roosevelt in 1943, held in Hot Springs, Virginia. At that meeting agreement was reached in principle on the establishment of an international organization dealing with food and agriculture. An Interim Commission was established and Dr Finn was made Chairman of its Fisheries Committee. The Committee worked over a period of 2 years along with other Committees of the Interim Commission. This work culminated in the establishment of the Food and Agriculture Organization (F.A.O.), a Specialized Agency of the United

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Nations, at a meeting in Quebec City, on October 16, 1945. (It was the first of the post-war Specialized Agencies to be established, with its own constitution and membership.) Dr Finn was appointed as the first Director of its Fisheries Division in 1946, a post which he held until his retirement in 1964.

The work of F.A.O. in fisheries, which is so well known around the world, got its start with Dr D. B. Finn. Indeed, had Dr Finn not been in Hot Springs there might not have been a Fisheries Division in its own right in F.A.O. The Constitution of F.A.O. states that "the term agriculture and its derivatives, include fisheries, marine products ...". Without doubt Dr Finn was one of the prime movers in getting recognition of the importance of fisheries as a source of food.

As Director of the Fisheries Department Dr Finn once again attracted talented people to his organization. Under his leadership F.A.O.'s Fisheries Division, which was later expanded to a full Department, came to be looked upon as the lead organization concerned with international fisheries. Its work began in the immediate post-war period and continued into a rapidly expanding world of emerging nations in Asia and Africa. (By the time of Dr Finn's retirement, membership of F.A.O. more than tripled from the original 39-member nations.) The Division's work included the establishment of regional fisheries commissions; the Yearbooks of Fisheries Statistics; the fishing boat and fishing gear congresses and technical assistance activities in developing countries, all of which have received worldwide recognition.

In his personal life Dr Finn was a highly cultured man with a great appreciation of music. Reserved in speech and manner, he came into his own through his marvelous tenor voice. He was a persuasive speaker and an excellent singer. Many informal gatherings during international fisheries meetings were enlivened by his rendition of "She's Like the Swallow" and "Foggy, Foggy Dew" which became part of fisheries lore. In 1964 Dr Finn retired with his wife Noel to their beloved 11th century "Castello" in Sterpeto, near Assissi, in the Umbrian countryside. He continued to attend some of the Fisheries meetings and to remain in touch with developments of later years. Family and friends came to visit him at the Castello from all over the world.

It had been D. B. Finn's early ambition to become a medical doctor. Instead, he became a scientist. Whatever youthful ambition he might have had for research, his talents were soon to be channelled into administration and fisheries development. With his talents for diplomacy and for attracting gifted and highly motivated scientists and technicians from various parts of the world, he was to affect fisheries research and development throughout the world. At Cambridge, his early mentor Sir William Hardy had said to him: "Finn, it is not your job to discover the truth, it's your job to get the people thinking about things." He took to heart the admonition and he not only got people to think about things, he got them to do things.

Dr Finn is survived by his wife Noel, son Julian, and daughters Gretchen and Fiona.

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Books received/Livres reçus

December/décembre 1982–January/janvier 1983

Advances in Marine Biology Volume 20. *Edited by J. H. S. Blaxter, Sir Frederick S. Russell, and Sir Maurice Yonge. Academic Press Inc., London and New York. 1982. 430 p. £35; $65.* In the first half of the book J. H. S. Blaxter and J. R. Hunter detail, review, and discuss "The biology of the clupeoid fishes." The second half concerns "Competition between fisheries and seabird communities" by R. W. Furness and "The scallop industry in Japan" by R. F. Ventilla. [R466]

Bivalve Culture in Asia and the Pacific: proceedings of a workshop held in Singapore, 16–19 February 1982. *Edited by F. Brian Davy and Michael Graham. International Development Research Centre, Ottawa, Ontario. 1982. 90 p. $5.* [R467]

Aquaculture Economics Research in Asia: proceedings of a workshop held in Singapore, 2–5 June 1981. *International Development Research Centre, Ottawa, Ontario. 1982. 128 p. $12.* The workshop, cosponsored by ICLARM (International Center for Living Aquatic Resources Management), considered microanalyses of existing and experimental production systems and the socioeconomics of aquaculture. [R468]

Freshwater Recreational Fishing: the national benefits of water pollution control. *William J. Vaughan and Clifford S. Russell with the assistance of Charles Paulsen and Richard Carson. Resources for the Future Inc., Washington, DC. Distributed by the John Hopkins University Press, Baltimore, Maryland. 1982. 222 p. $12 (paperback).* This book presents estimates of the benefits of water pollution control in the freshwater fishing category. [R469]

Polychaetes Recorded Near Two Pulp Mills on the Coast of Northern British Columbia: a preliminary taxonomic and ecological account. *Judith A. Fournier and Colin D. Levings. Syllogeus 40. National Museum of Natural Sciences, Ottawa, Canada. 1982. 91 p.* Sampling from 1972 to 1975 produced 166 taxa of polychaetes including new records, 34 for British Columbia and possibly 6 new to science. [R470]

Aquatic Biota of Mexico, Central America and the West Indies. *Edited by Stuart H. Hurlbert and Alejandro Villalobos–Figueroa. A copy may be ordered with payment to "Aquatic Biota — SDSU Foundation" addressed to Stuart H. Hurlbert, Department of Biology, San Diego State University, San Diego, California 92182. 1982. xv + 529 p. $20 (U.S.).* This is the third and final volume of the series which is intended to serve as reference manuals. The work is a compilation of selective taxonomic bibliographies for the fauna and flora of inland waters of Mesoamerica and the Caribbean region; the bibliographies were contributed by 150 biologists. [R471]

ANNOUNCEMENTS/AVIS

Aquatic Toxicity Workshop

The 10th Annual Aquatic Toxicity Workshop will be held on November 7–10, 1983, at the Lord Nelson Hotel, Halifax, Nova Scotia. This is a continuing series covering topics from basic research to applications in environmental monitoring, setting of regulations and guidelines, and forming water control criteria. Emphasis is on informal exchange of ideas and information on aquatic and environmental toxicology in Canada. Sessions will consist of a series of contributed papers, posters, and workshops. Topics will include aquatic toxicology (especially marine), acid rain, hazard assessment, and control of toxic substances.

For further information please contact *R. F. Addison or P. G. Wells, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2*; (902) 426-3279 or (902) 426-3276.

Atelier sur la toxicité aquatique

Le 10e Atelier annuel sur la toxicité aquatique se tiendra à l'hôtel Lord Nelson, de Halifax, en Nouvelle-Écosse, du 7 au 10 novembre 1983. Cette série continue de réunions couvre un éventail de sujets allant de la recherche fondamentale à ses applications à la surveillance de l'environnement, à l'élaboration de règlements et de lignes directrices, et à la définition de critères de contrôle de l'eau. On met l'accent sur un échange informel d'idées et sur l'information en toxicologie aquatique et environnementale au Canada. Les séances comporteront communications, affiches et ateliers de travail. Parmi les sujets traités, notons la toxicologie aquatique (surtout marine), les pluies acides, l'évaluation des dangers pour l'environnement et le contrôle des substances toxiques.

Pour plus amples renseignements, on est prié de s'adresser à *R. F. Addison ou P. G. Wells, Laboratoire d'écologie marine, Institut océanographique de Bedford, Dartmouth (Nouvelle-Écosse) B2Y 4A2;* (902) 426-3279 ou (902) 426-3276.

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Articles

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Analysis of multiple objectives in Oregon coho salmon policy **K. D. Walker, R. B. Rettig, and R. Hilborn**

Community gradients in the Scotian Shelf zooplankton **M. J. Tremblay and J. C. Roff**

Effects of changes in pH on transparency and thermal regimes of Lohi Lake, near Sudbury, Ontario **N. D. Yan**

Energy metabolism in a rapidly developing marine fish egg, the red drum (*Sciaenops ocellata*) **R. D. Vetter, R. E. Hodson, and C. Arnold**

Optimizing survey design for determining age structure of fish stocks: an example from British Columbia Pacific herring (*Clupea harengus pallasi*) **J. F. Schweigert and J. R. Sibert**

Anthropogenic zinc and cadmium burdens in sediments of selected southern Ontario lakes **H. E. Evans, P. J. Smith, and P. J. Dillon**

Adaptive probing strategies for age structured fish stocks **D. Ludwig and R. Hilborn**

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Measurements of benthic macroinvertebrate standing crop from the Canadian continental shelf and slope of southern Davis Strait and Ungava Bay **P. L. Stewart**

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Silicon contamination in diatom nutrient enrichment experiments **S. J. Tarapchak, D. R. Slavens, M. A. Quigley, and J. S. Tarapchak**

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